Estimating characteristic length scales of dynamic biological systems: removing the need for long time series

Jessica Trebilco B.Sc

Research Thesis submitted in partial fulfilment of the requirements for a Bachelor of Science with Honours

School of Zoology
University of Tasmania
2002

ACKNOWLEDGMENTS

Thank you to Craig Johnson, Simon Wotherspoon, Rebecca Habeeb and Piers Dunstan for their continued advice and support. Thanks also to Andrew Greenhill, Nepelle Temby and Nikki Green for keeping me sane!

Analyses in this thesis were performed using programs developed by Simon Wotherspoon from the School of Mathematics and Physics, University of Tasmania.

ABSTRACT

The choice of appropriate spatial scales for observing, conserving and managing systems are pervading questions in applied ecological research. Determining the characteristic length scales (CLSs) of ecological systems is likely to provide valuable information towards answering these questions. The CLS is the scale at which the ratio of deterministic signal to noise in a system's dynamics is maximised i.e. the scale that captures the meaningful signal in the system's dynamics. Recent methods for identifying the CLS are attractive because they accommodate the complex non-linear behaviours that occur in ecological systems. However, these methods require long temporal data series and so are unrealistic for most natural systems.

This thesis develops and examines two alternatives to using long time series data to estimate CLSs. The first is a short time series approach that requires data from only three or four consecutive landscapes. The second approach uses spatial data from a single point in time. The performance of these methods is compared with current techniques, using data from spatial competition systems. The model systems employed in this study are more complex than models examined by previous authors and provide a better indication of how CLSs might perform with real data sets.

Results indicate that the short time series approach to estimating CLSs is more consistent in its interpretation than the long time series method, and has great potential for application to natural systems. A comparison of CLS results with more conventional analyses for identifying scales of spatial pattern (variograms and nested ANOVA) suggests that a combination of the two approaches may be most successful for defining characteristic scales in applied ecological contexts.

TABLE OF CONTENTS

LIST OF FIGURES AND TABLES

INTRODUCTION

The identification of 'characteristic length scales' (CLSs) in ecological systems has been an important, albeit elusive, goal in ecology (Wiens 1989, Levin 1992, Lawrie and McQuaid 2001, Bishop *et al.* 2002). Ideally, the CLS is an objective estimate and measurements at this scale capture the most important aspects of a system's dynamics. CLSs have important potential applications for several key scale-related issues in ecology such as defining conservation areas for habitats and communities (Castilla 2000), determining the appropriate sizes of management units for living resources (Garcia-Charton and Perez-Rufaza 1999), and providing suitable scales for observing meaningful changes in ecosystem state (Underwood and Chapman 1998).

Grieg-Smith (1952), Kershaw (1957) and others first explored characteristic spatial scales in ecology by developing methods to determine patch sizes in vegetation. Since the 1950s, scales of spatial pattern have been investigated using numerous techniques, most involving some form of variance spectrum (e.g. Weigert 1962, Levin and Buttel 1986, O'Neill *et al.* 1991, De Roos *et al.* 1991). One crucial problem with most of these approaches is that they ignore the dynamic properties of ecological systems by describing only static spatial patterns. It follows that these measures cannot accommodate the complex non-linear oscillations and non-uniform patterns in spatial variance that are common in Nature (Turchin and Taylor 1992, Ellner and Turchin 1995).

The CLS concepts of Rand and Wilson (1995), Keeling *et al.* (1997) and Pascual and Levin (1999) were developed to accommodate the dynamic nature of ecological systems. These authors have defined the CLS as the spatial scale at which the ratio of deterministic signal to noise in a system's dynamics is maximized. The underlying tenet for this definition is that the amplitude of temporal fluctuations in ecological systems changes with the scale of observation. If a bounded system is viewed though different sized 'windows', then we expect to see pronounced, noisy fluctuations in small windows, while in larger windows fluctuations will be averaged out. The CLS of the system is some intermediate window size, where the fluctuations over time reflect meaningful trends. This is an appropriate scale for observing the deterministic dynamic of the system.

Rand and Wilson (1995) identified the scale of 'maximum non-trivial determinism' for a model predator-prey system as the window size above which there is no proportional increase in variance. Keeling *et al.* (1997) noted that Rand and Wilson's (1995) method is based on a long-term system average and that it is therefore only appropriate for systems that are statistically stationary. Keeling *et al.* (1997) modified Rand and Wilson's (1995) approach by modelling the long-term behaviour of systems using techniques from non-linear time series analysis.

Pascual and Levin (1999) also suggested a CLS estimation technique suitable for ecological systems, but their approach to identifying the scale of maximum determinism to noise ratio is more direct. At a given window size, the degree of determinism is evaluated from the accuracy of a predication algorithm (Kaplan and Glass 1995) established using non-linear time series analysis. The techniques of Keeling *et al.* (1997) and Pascual and Levin (1999) are attractive since they accommodate the complex oscillatory behaviours present in many ecological systems.

The potential ecological applications of these techniques are exciting. However, CLSs have so far been estimated for a limited number of model biological systems (Rand 1994, Rand and Wilson 1995, Keeling *et al.* 1997, Pascual and Levin 1999, Wilson and Keeling 2000). There are two fundamental issues to be addressed before these approaches to estimating CLSs can make the important transition from theoretical to applied ecology. First, because Pascual and Levin's (1999) and Keeling *et al.*'s (1997) techniques are new, their performance and robustness need to be evaluated for a range of systems. The second and more important hurdle is that the non-linear time series techniques adopted by Keeling *et al.* (1997) and Pascual and Levin (1999) require extremely long time series of spatially resolved data. While these data are readily obtainable from computer models, they are generally not available for natural systems. If CLSs are to be measured for real ecological systems, then the current data requirements must be modified.

This thesis develops and examines two alternatives to the use of long time series for estimating CLSs. The first alternative is to substitute long time series with multiple short time series, obtained from windows at different positions on a landscape. Solé and Bascompte (1995) introduced a similar approach for identifying chaos in ecological systems. This approach provides a dramatic reduction in data requirements from several thousand time steps

to only three or four consecutive landscapes. The second alternative is more extreme and uses data from a single point in time. In terms of sampling effort, this is the most desirable alternative. The approach assumes that it is possible to substitute time series data with a spatial series obtained by 'sliding' windows of observation across a landscape. The sliding window sampling method is the 2-dimensional equivalent of Plonick *et al.*'s (1996) "gliding box" method. Replacing temporal data with spatial data is justified if the dynamics of distant parts of the landscape are out of phase, representing different stages of the system's overall dynamic.

These two novel approaches – short time series and sliding windows – are evaluated and compared with the original techniques of Keeling *et al.* (1997) and Pascual and Levin (1999) based on long time series. CLS techniques are also compared with two more conventional spatial analyses: variograms (e.g. Palmer 1988, Rossi *et al.* 1992, Dent and Grimm 1999) and hierarchical ANOVA (e.g. Underwood 1981, Morrisey *et al.* 1992, Swadling *et al.* 1997).

METHODS

An outline of existing techniques for estimating CLSs

The techniques of Rand and Wilson (1995), Keeling *et al.* (1997) and Pascual and Levin (1999) estimate CLSs by comparing measures of variance in the dynamics at different spatial scales of sampling. Given a time series of landscapes composed of pixels L_{ij}^t (i and j are coordinates on the landscape), the density of a given species X in a 'window' of side length l is $X_l^t = \frac{1}{l^2}\sum_{i=1}^{l}\sum_{j=1}^{l} L_{ij}^t$

Rand and Wilson (1995) resolve the scale of maximum determinism to noise ratio using variance spectra. They plot

$$l^2 Var\left(X_l^t\right) = l^2 E_t\left[\left(X_l^t - \overline{X}_l^t\right)^2\right]$$

against l^2 and define the CLS as the scale where the graph asymptotes. In this notation, $E_t(Z)$ indicates the expectation of any variable Z over interval t, for example $\overline{X}_l^t = E_t\left(X_l^t\right)$ is the long-term average of X_l^t. Since Rand and Wilson's (1995) measure is designed for non-oscillatory systems, it is not surprising that the measure performed poorly for model systems used in the current study (described in the final section of the methods). Graphs of $l^2 Var\left(X_l^t\right)$ versus l^2 are not presented in the results.

Keeling *et al.* (1997) modified Rand and Wilson's (1995) measure by replacing the long-term average $\overline{X}_l^t$ with the predicted value $\hat{X}_l^t$ of X_l^t, where $\hat{X}_l^t$ is determined from non-linear time series analysis (described in the following section). Keeling *et al.*'s (1997) measure is

$$Error\ X = l\sqrt{E_t\left[\left(X_l^t - \hat{X}_l^t\right)^2\right]}$$

Error X is plotted against l, and the CLS is indicated where the graph plateaus. This is the "size of almost independent windows" (Keeling *et al.* 1997).

Pascual and Levin (1999) developed a more direct approach to identifying the scale of 'maximum non-trivial determinism'. They scale the variance in predicted values $\hat{X}_l^t$ by the time series variance at a given window size. Pascual and Levin's (1999) measure is

$$prediction\ r^2 = 1 - \frac{E_t\left[\left(X_l^t - \hat{X}_l^t\right)^2\right]}{Var\left(X_l^t\right)}$$

As the ratio of determinism to noise increases (with changing window size), the error in prediction decreases. The scale at which *prediction* r^2 is maximized is the CLS. Pascual and Levin (1999) point out that their measure is likely to indicate a smaller CLS than Keeling *et al.*'s (1997) *error X*, because maximum predictability can occur before the onset of independence of windows.

Describing complex dynamics with non-linear time series analysis

The key feature of the approaches of Keeling *et al.* (1997) and Pascual and Levin (1999) is that they take into account complex non-linear behaviour in the deterministic dynamic. Complex signals are described using non-linear time series analysis, which involves two steps: (i) reconstruction of the dynamics of the system, and (ii) characterisation of the reconstructed dynamics (Kaplan and Glass 1995). Both Keeling *et al.* (1997) and Pascual and Levin (1999) use Takens' (1981) technique of attractor reconstruction for (i). Takens (1981) showed that the general shape of a multispecies system dynamic (the attractor) can be reconstructed in *n*-dimensional phase space using time series data from a single observed variable X_t. A reconstructed attractor is topologically equivalent to the real state space attractor that could be obtained by measuring all variables in the system.

While there are several approaches to attractor reconstruction (Abarbanel 1996, Kantz and Schrieber 1997) both Keeling *et al.* (1997) and Pascual and Levin (1999) use the technique of time delay embedding. Given time series data for a single species X_t, time-delayed coordinates of the reconstructed attractor are

$$X_t,\ X_{(t-\tau)},\ X_{(t-2\tau)},\ \ldots,\ X_{(t-(d_E-1)\tau)}$$

In this representation, τ is some selected time delay and d_E is the embedding dimension that defines the dimensionality of the phase space in which the attractor is reconstructed. For example, in the time series $X_1, X_2, X_3, \ldots, X_{10}$, an embedding with $\tau = 2$ and $d_E = 2$ has points $(X_1, X_3), (X_2, X_4), (X_3, X_5), \ldots, (X_8, X_{10})$ in reconstructed 2-dimensional phase space.

Appropriate values for τ and for d_E can be estimated from the time series data itself. Pascual and Levin (1999) select τ as the value for which the autocorrelation function first crosses

zero. Autocorrelation measures correlations between coordinates at different values of τ, and the zero crossing of this function is an indication of the time delay for which coordinates are independent but still dynamically linked. Tong (1990) offers a convincing criticism of applying the linear autocorrelation function for non-linear analysis. Abarbanel (1996), Kantz and Schreiber (1997) and Nichols and Nichols (2001) advocate the use of Fraser and Swinney's (1986) mutual information function (the non-linear equivalent of autocorrelation) to determine an optimal value for τ. For the following analyses, τ is selected as the delay at which the mutual information function reaches its first minimum. The embedding dimension d_E is chosen as the embedding dimension in which the percentage of false nearest neighbours (FNN) falls within some small threshold of zero (Kennel *et al.* 1992). This is a widely accepted approach for selecting d_E in systems with dynamical noise (Abarbanel 1996, Kantz and Schrieber 1997).

Step (ii) of non-linear time series analysis involves quantifying the degree of determinism in reconstructed dynamics. An algorithm based on *k*-nearest neighbours (Kaplan and Glass 1995) is used to obtain predicted values $\hat{X}_t$ from the reconstructed attractor. The value of a point X_t after a lag of h time steps is X_{t+h}. A predicted value of X_{t+h} is obtained by taking a weighted average of the trajectories of X_t's closest neighbouring points in phase space: $X_{t1}, X_{t2}, X_{t3}.....X_{tk}$. Predicted values are calculated for each point on the attractor, with h set equal to the time delay τ. The accuracy of predictions indicates the degree of determinism in the system's dynamics.

Alternatives to attractor reconstruction from long time series

The concern of this thesis is that attractor reconstruction using long time series is impractical for real ecological systems because the data requirements cannot be met. Accordingly, two alternative methods are examined which have realistic data requirements for ecological applications. The first is attractor reconstruction using data from three or four consecutive landscapes, which is referred to as the 'short time series' approach. A second, more extreme approach to reducing data requirements is to substitute time series data with spatial data from a single point in time. This is referred to as the 'sliding window' method. The motivation underpinning both approaches is that data from multiple locations in space may provide similar information to data collected at a fixed location over a long time series (Solé and Bascompte 1995).

Short time series

In this approach, multiple short time series are embedded to reconstruct a system's attractor piece-wise (Fig 1). To generate multiple time series, the entire landscape must be sampled at each time step. On a cellular landscape (i.e. a landscape consisting of a large but finite array of contiguous cells where each cell can exist in a single state) this is achieved by observing the dynamics in successive windows separated by a single cell's width, horizontally or vertically. The embedding parameters τ and d_E for attractor reconstruction are not determined in the same way as for long time series analysis. According to Kantz and Schreiber (1997), any value of τ should suffice for an embedding, although there tends to be some optimal delay. Since consecutive landscapes are generally easier to sample in ecological applications, results are presented for delay $\tau = 1$. The number of embedding dimensions d_E is the number of landscapes sampled minus one, as the final landscape provides a data set against which the accuracy of predictions is assessed. Embeddings from different numbers of landscapes are evaluated in the results.

A key assumption of the short time series approach is that all parts of the sampled area lie somewhere on the same attractor. If this is not the case, more than one attractor may be reconstructed in the same phase space which will create problems with predictions. While the assumption also applies to the original time series methods (Keeling *et al.* 1997, Pascual and Levin 1999), it is only of concern for these techniques at large window sizes. It is generally certain that a single attractor is sampled for model systems, but this may be much harder to establish for a real ecological system.

Sliding windows

The sliding window sampling method also generates multiple short data series to reconstruct an attractor in sections (Fig 2). A single landscape is sampled by sliding windows of observation cell by cell, horizontally across the landscape. Each data series begins one cell lower than the previous series so that the whole landscape is sampled. Attractor reconstruction from a spatial series assumes that spatial data capture the general shape of the system's dynamics in the same way as do time series data. The assumption is reasonable if distant parts of the landscape are out of phase, that is, they are on different parts of the system's attractor. Because of the large model landscapes used in the current study, this assumption is met for all analyses.

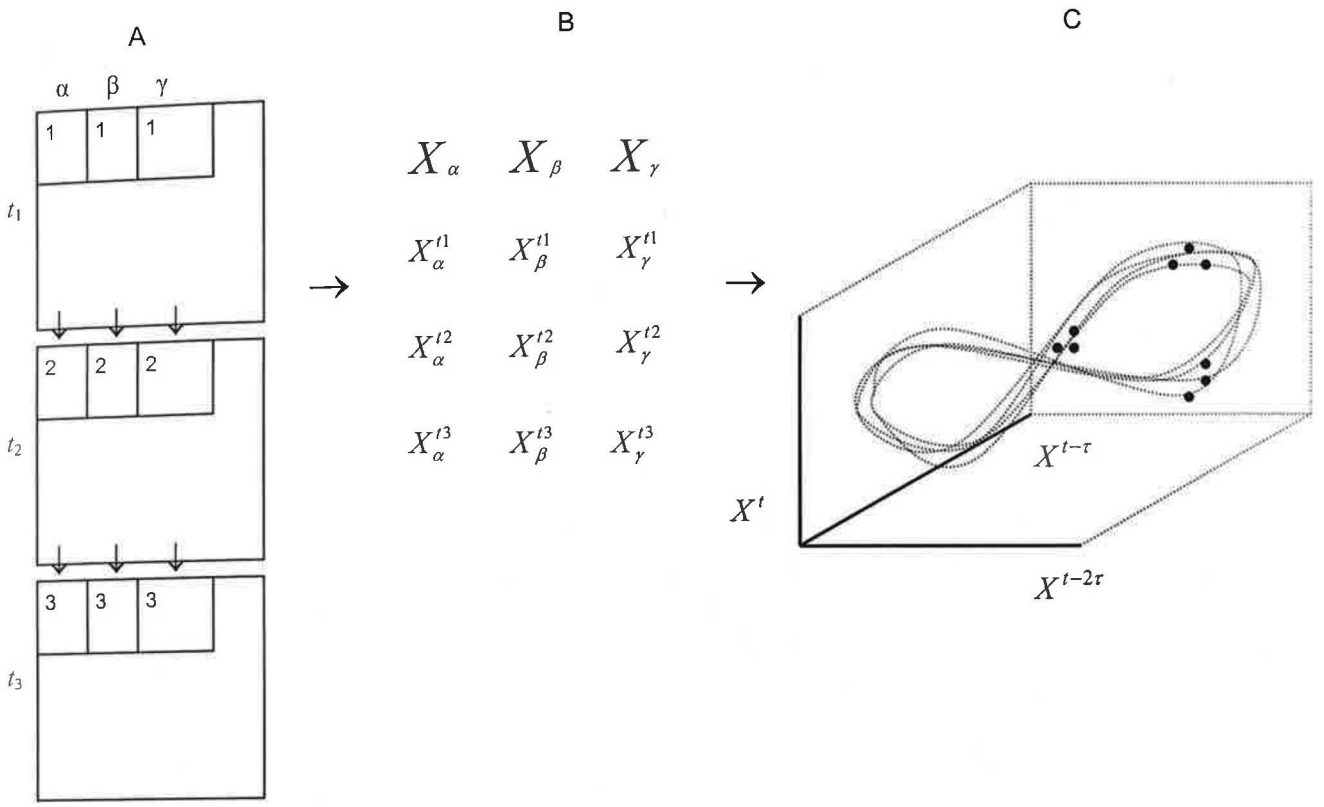


Figure 1 The short time series approach to attractor reconstruction. The large square represents an entire landscape, while the small squares represent windows of observation on the landscape. **A** This approach requires a temporal sequence of only three or four consecutive landscapes. At each time step the entire landscape is sampled, with successive windows separated by a single cell, horizontally or vertically. In this representation there are three time steps t_1,t_2 and t_3, and three data series at position α, β and γ. **B** Three short time series are generated, with X^t_α indicating the density of species X at time t and at position α on the landscape. **C** The system's attractor is reconstructed piece-wise using the delayed coordinates X^t, $X^{t-\tau}$, $X^{t-2\tau}$, where $\tau = 1$. Thus, for a window α, the point in reconstructed phase space is given by $(X^{t1}_\alpha, X^{t2}_\alpha, X^{t3}_\alpha)$.

Methods developed for long time series to identify embedding parameters are not appropriate for reconstructing attractors from spatial data series. A modified false nearest neighbours (FNN) algorithm was used here to select appropriate embedding dimensions. Because there are many more points in sliding window embeddings than in conventional attractor reconstructions, computing the percentage of false nearest neighbours for every point in the embedding takes too long. Thus, the FNN algorithm is computed for a random sample of 1000 data points. Computing *k*-nearest neighbour predictions for every data point in a sliding window embedding is similarly slow and so these predictions are also based on a random sample of 1000 points. Note that random samples were used for *k*-nearest neighbour predictions in the previous short time series approach.

There are two sensible alternatives for selecting the spatial delay, τ. One approach is to use the same delay for every window size, as for the time series embeddings. However, in the sliding window approach to attractor reconstruction, the units of embedding delay are cells rather than time steps. Thus, a potential problem with using delays of a fixed number of cells is that successive embedding dimensions will have greater overlap of data at large window sizes than at small window sizes, which could bias CLS statistics. A second alternative is to use delays set as some proportion of the linear dimensions of the window, $\tau = 1/n \times$ window length, provided that this proportion is some whole number of cells.

Fixed delays and proportional delays are evaluated in this thesis by assessing their performance for the 'null case': random landscapes composed of independent, discrete valued pixels. In this null case, we expect the ratio of determinism to noise to be fixed across different window sizes so that *prediction* r^2 and *error* X are constant (see Appendix for proof and empirical verification).

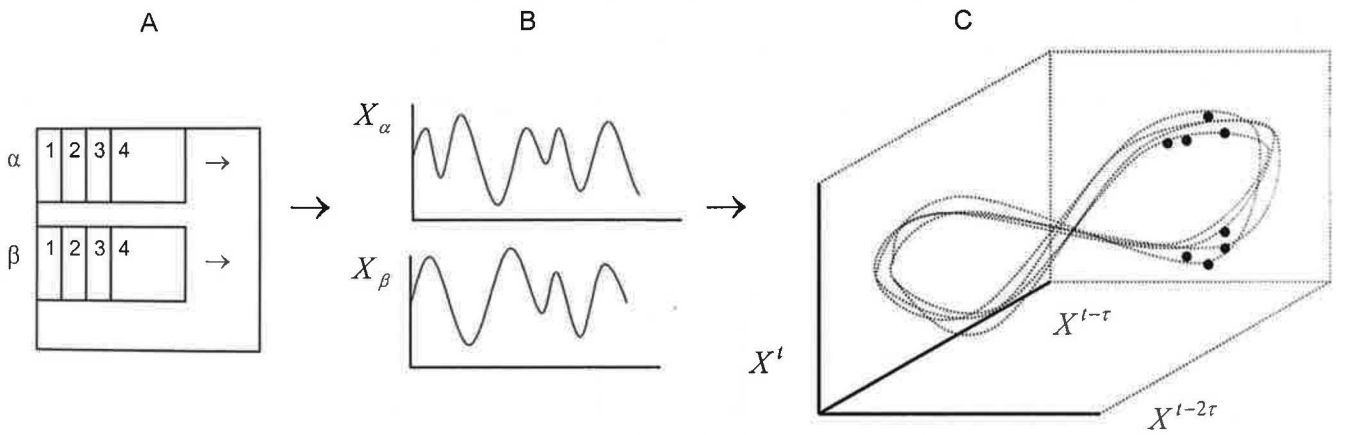


Figure 2 The sliding window method of attractor reconstruction. The large square represents an entire landscape, while the small squares represent windows of observation on the landscape. **A** Multiple short data series are generated by sliding windows horizontally across the landscape, so that the entire landscape is sampled. The sequence in each data series as the window of observation slides across the landscape is indicated as 1,2,3,4... Two data series are shown at positions α and β. **B** The data series X_α and X_β represent different sections of the system's attractor. **C** The attractor is reconstructed piece-wise using the delayed coordinates X^t, $X^{t-\tau}$, $X^{t-2\tau}$.

Conventional methods of spatial analysis

There are numerous statistical methods that have been used to identify the scale of spatial pattern in ecological systems. Here, the results of two widely used static spatial methods are

compared with CLS estimates. The first method is variogram analysis, which has been critically evaluated in an ecological context (Palmer 1988, Rossi *et al.* 1992, Dent and Grimm 1999). Variograms plot the variance in abundance of a given species at different distances or spatial lags on a landscape. The plateau on a variogram plot indicates the scale of spatial pattern for that species. For the current purpose, lags have been limited to the horizontal or vertical direction to enhance computational speed. A modified approach based on presence/absence data rather than abundance data is used to examine variance between individual cells in the model systems.

The second spatial approach is nested analysis of variance (ANOVA) of landscape data sampled at a hierarchy of spatial scales (Fig 3). Results are interpreted with an emphasis on effect size (where the effects are spatial scales), rather than significance. Nested ANOVA has been applied and evaluated in ecological applications for identifying spatial scales of greatest and least variance in species abundance (e.g. Underwood 1981, Morrisey *et al.* 1992, Swadling *et al.* 1997, Dunstan and Johnson 1998, Graham and Edwards 2001). Analyses in this thesis use a fully random effects model and negative variance components are treated as zero. The effect size is estimated by expressing variance components as proportions of the total variance. These proportions are plotted against spatial scale to identify important scales of spatial pattern.

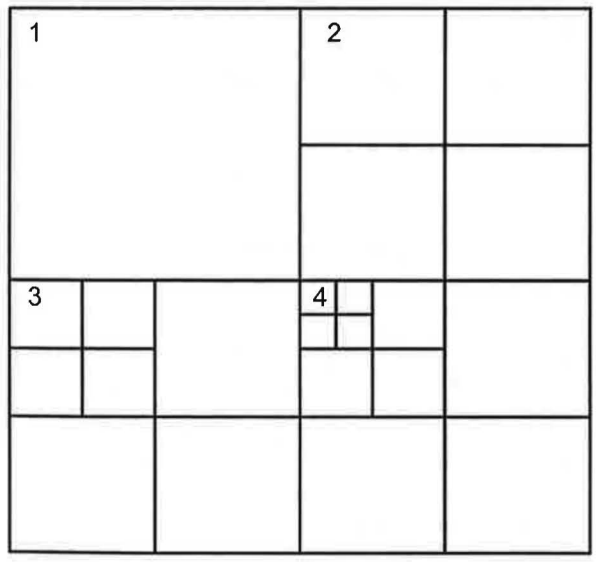


Figure 3 Method for hierarchical landscape sampling. The landscape is represented by the largest square. There are four spatial scales for analysis, indicated by numbering in the top left box at each scale.

The models

Data were generated using four spatially explicit (cellular automaton) model systems from the *Compete* software (Johnson 1997). Three of these models are spatial competition systems of hypothetical assemblages of 3-, 6- and 12-species of sessile organisms (Johnson 1997, Johnson and Seinen 2002), while the fourth model is a coupled lattice model of a real coral reef community (Johnson and Dunstan 2002).

The three hypothetical systems demonstrate self-organisation at a variety of spatial scales (Figs 4 & 5). Spatial patterns in these models emerge as a result of simple and symmetrical interaction networks containing intransitive loops. The intransitive loop defining the 3-species system is an ecological equivalent of the 'rock-paper-scissors' network. This network can be represented as $S_1 > S_2 > S_3$ where $S_x > S_y$ indicates that S_x is the superior competitor and overgrows S_y in a competitive interaction.

The 6- and 12-species systems show self-organisation at two spatial scales. The interaction networks defining these systems are $S_6 > (S_5\, S_4)$, ..., $S_1 > (S_6\, S_5)$ for the 6-species system and $S_{12} > (S_{11}\, S_{10}\, S_9)$, ..., $S_1 > (S_{12}\, S_{11}\, S_{10})$ for the 12-species system. In this notation, $S_x > (S_y\, S_z)$ indicates that S_x will overgrow both species S_y and S_z in a competitive interaction. Figures 4 and 5 illustrate spatial clustering of species colonies in these models: two groups of three species in the 6-species system and three groups of four species in the 12-species system. While the same species always group together, there is oscillation in the dominance of mulit-species groups over long time series. Dominance of specific groups varies randomly depending on initial random configuration of 'recruits' at generation zero, and arises as an artefact of finite landscape size. It is less obvious with very large landscapes.

The coral reef model is more complex than a simple cellular automaton because parts of colonies, or whole colonies may die (a colony is a set of juxtaposed cells of the same species type). There are twelve physiognomic life forms in the model (Fig 4D) and neighbour specific growth rates, interaction outcomes, mortality and recruitment have been parameterised from direct observations of communities on the Great Barrier Reef. In this model the emergent pattern of community composition matches the pattern from the real system after an appropriate period without a major disturbance event (Johnson and Dunstan 2002). Three physiognomic groups have been selected for analysis. These are (i) the dominant turf and coralline algae (referred to hereafter as turf algae), (ii) the corymbose and digitate

Acroporidae, and (iii) the Faviidae. Coral groups (i) and (ii) occur at lower densities than the turf algae, with favids occupying the smallest patches (Fig 5D).

There are several important differences between the models used in the current study and the models for which CLSs have previously been estimated. The *Compete* systems contain more species than systems analysed by Rand (1994), Rand and Wilson (1995), Keeling *et al.* (1997), Pascual and Levin (1999) and Wilson and Keeling (2000). A second difference is that the 6- and 12-species models used here show more than one scale of spatial pattern formation and these models are therefore more interesting for spatial analysis. Finally, the coral reef model gives a useful indication of how CLS estimation techniques might perform with data from real ecosystems.

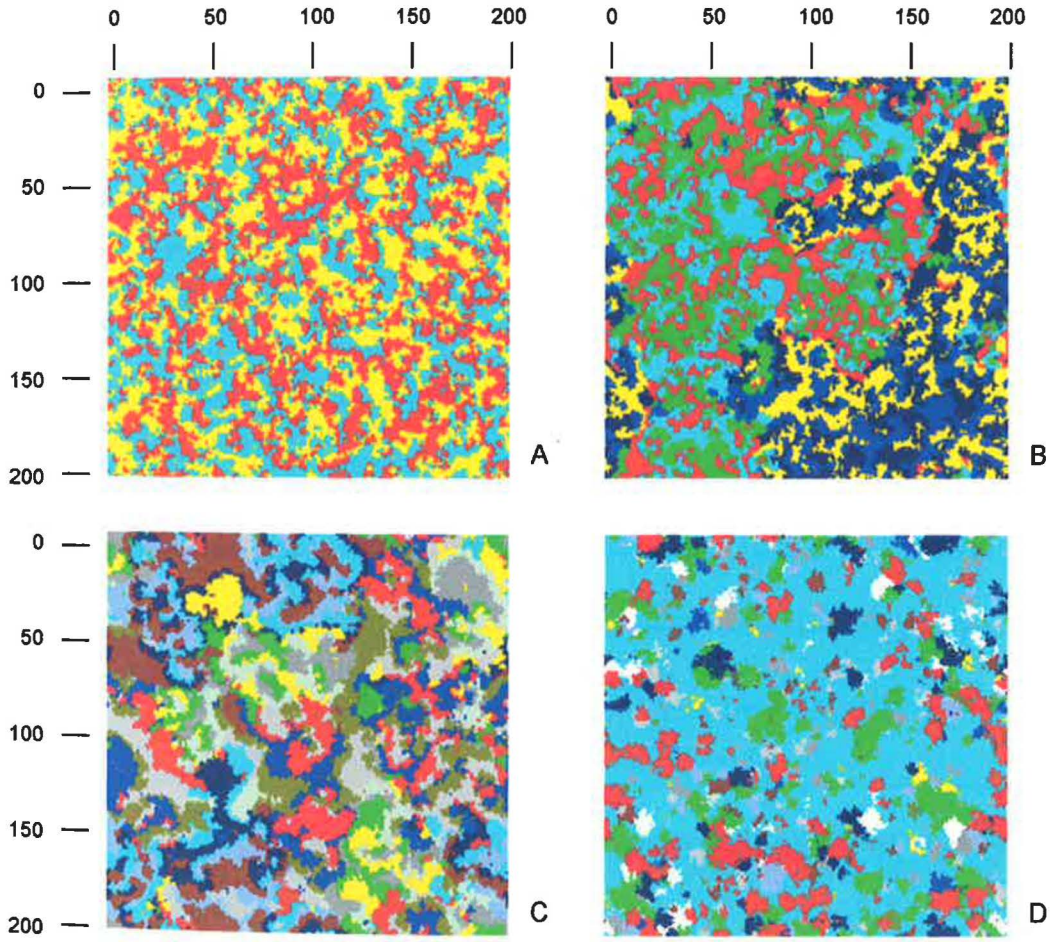


Figure 4 Representative landscapes from the four model systems used to generate data. Images **A** – **D** show the 500th generation from model runs with random initial configurations of recruits at generation zero. Landscape size is 200 × 200 cells in all cases. **A** 3-species system. **B** 6-species system with two groups of three species and two scales of spatial self-organising. **C** 12-species system with three groups of four species and two scales of spatial self-organising. **D** Coral reef system with twelve physiognomic groups. Groups selected for later analyses are the dominant turf algae (light blue), digitate and corymbose Acroporidae (red patches) and Faviidae (dark grey patches).

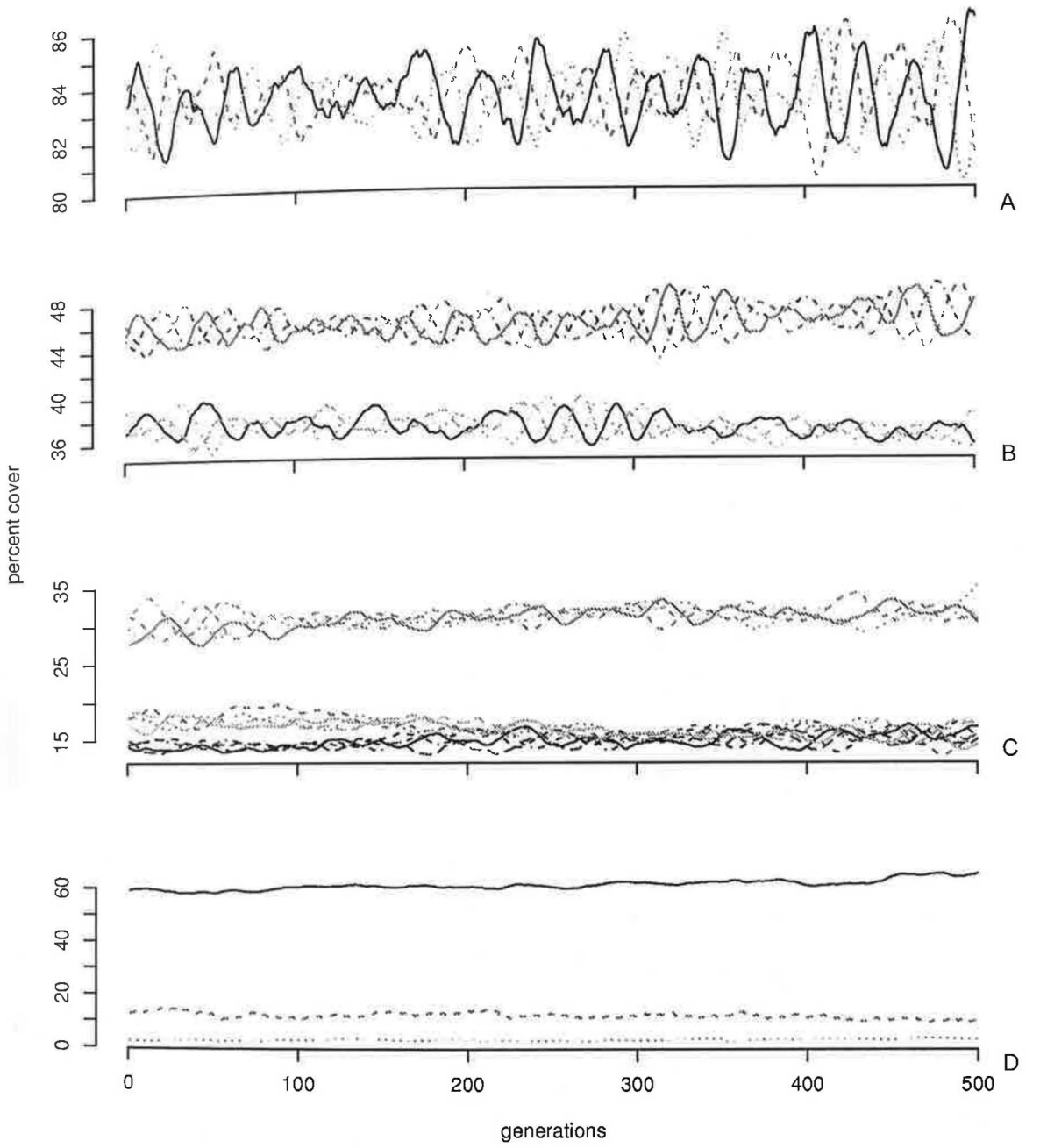


Figure 5 Changes in percent cover over 500 generations for the four model systems. **A** 3-species system. **B** 6-species system which self-organises into two groups of three species. The dominance of one group of three species is an artefact of finite landscape size and the identity of the dominant group varies between model runs. **C** 12-species system which self-organises into three groups of four species. As in the 6-species system, the identity of the dominant four species group depends on the initial random configuration. **D** Coral reef system with three of a total twelve physiognomic groups represented. Turf algae (solid line), digitate and corymbose Acroporidae (dashed line) and Faviidae (dotted line).

RESULTS

Evaluation of long time series methods

To provide a basis for comparison with the short time series and sliding window techniques, and because the approaches of Keeling *et al.* (1997) and Pascual and Levin (1999) have thus far only been applied to a limited number of simple models, the CLSs of the four models were first estimated using original long time series approaches. For the simple 3-species system, all three species gave similar results and trends were consistent between model runs with different initial random configurations of recruits. A CLS of approximately 20 cells length is indicated by the graph of *prediction* r^2 (Fig 6A). *Error X* suggests a larger scale of around 40 cells length (Fig 6B).

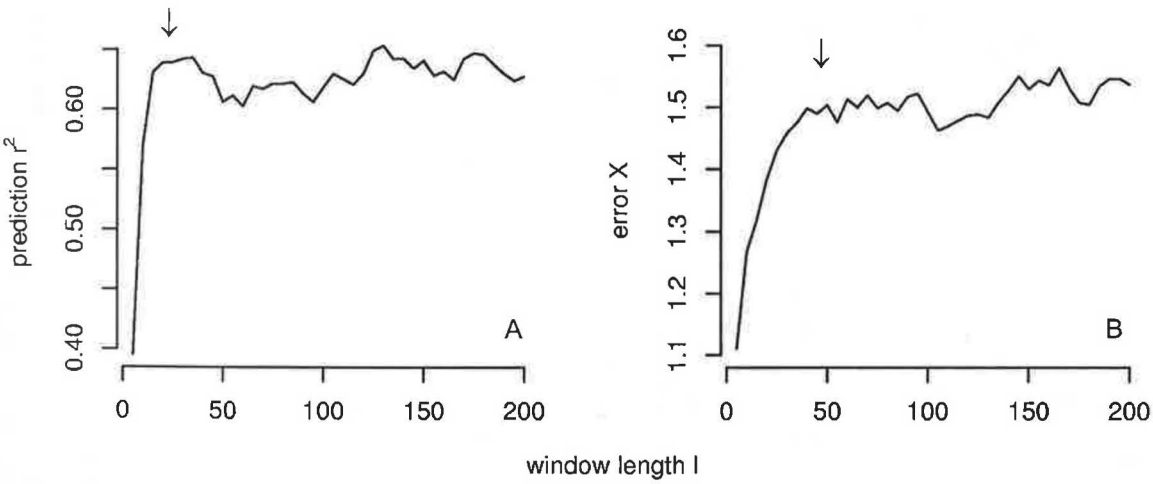


Figure 6 CLSs estimated for the 3-species system using long time series data for species 1. **A** *prediction* r^2 (Pascual and Levin 1999), **B** *error X* (Keeling *et al.* 1997). The analysed time series contains 10000 data points sampled at each time step, with the first 200 time steps discarded. Landscape size is 500 × 500 cells. Time delay $\tau = 9$, embedding dimension $d_E = 6$, number of nearest neighbours $k = 10$. Similar results were obtained for species 2 and 3 in this system. Arrows identify approximate CLS values.

Unlike in the 3-species system, for the 6-species system the shape of *prediction* r^2 and *error X* curves depends strongly on initial conditions (Fig 7). However, it is unclear how these shapes relate to specific differences in spatial dynamics between runs, for example whether some species have higher densities than others. A notable feature is that curves for the six species cluster into two groups of three. The same species cluster together spatially in *prediction* r^2 and *error X* graphs as they do on the model landscape. CLSs for the 6-species system

estimated from Pascual and Levin's measure are within the range of 30 – 70 cells. Unambiguous identification of CLSs using *error X* is problematic.

Long time series analyses for the 12-species system (Fig 8) produced similar trends to those observed for the 6-species system. Species cluster into three groups of four in the CLS plots, again forming the same groups that cluster spatially on the landscape. Also similar to the 6-

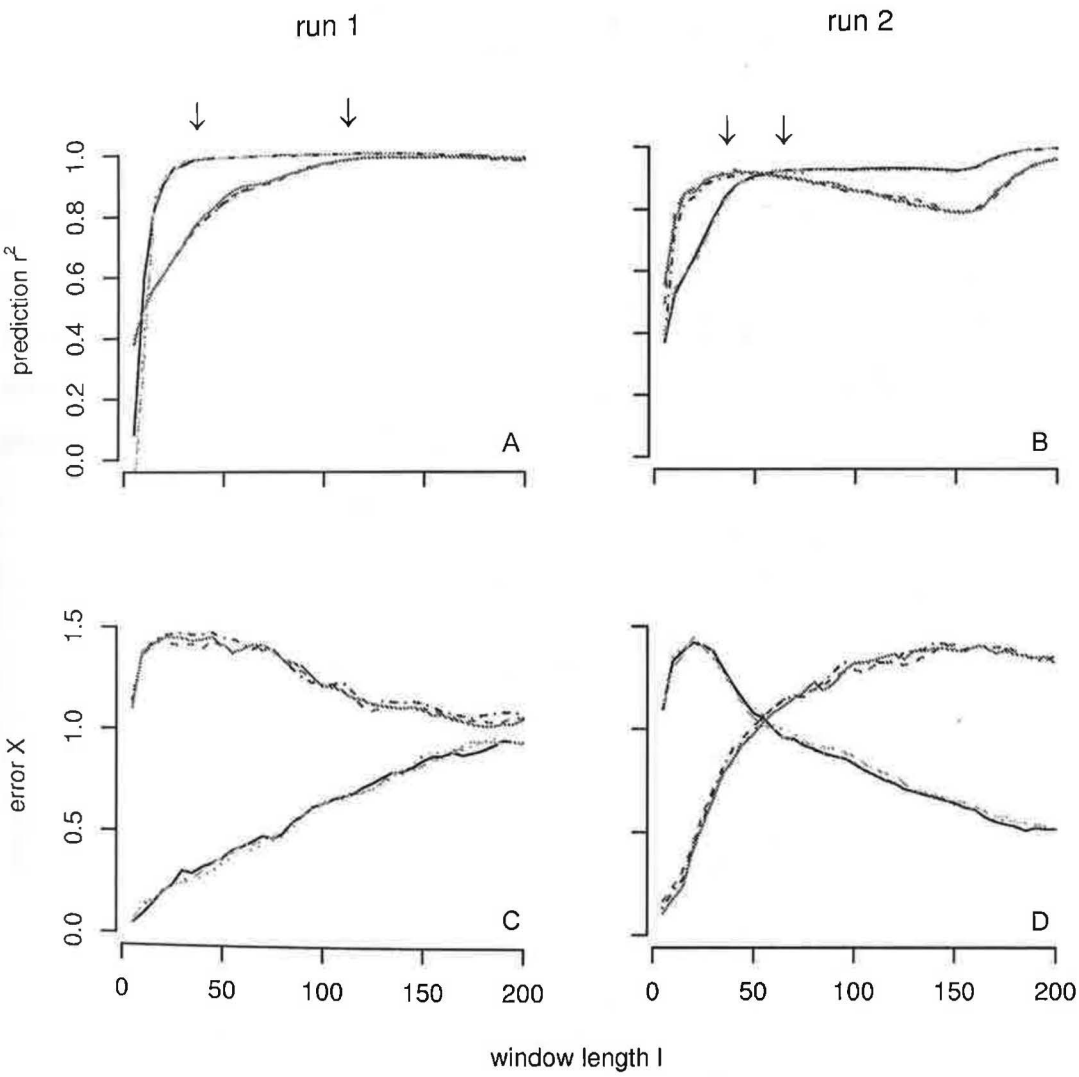


Figure 7 CLSs estimated for the 6-species system using long time series data for all species (represented here by different dashed lines). Examples from two model runs with different initial random configurations of recruits are presented (**A** & **C** run 1, **B** & **D** run 2). **A** & **B** *prediction* r^2, **C** & **D** *error X*. The analysed time series contains 10000 data points sampled at each time step, with the first 200 time steps discarded. Landscape size is 500 × 500 cells. $\tau = 12$, $d_E = 6$, $k = 10$. Arrows identify approximate CLS values. Differences in CLSs indicated by groups of three species (as in **A** & **B**) do not consistently correspond with 'winning' and 'losing' groups over the time series.

species system, there was notable variability in *prediction* r^2 and *error X* curves between model runs. The estimated CLS range from Pascual and Levin's measure is 30 – 60 cells. It is difficult to interpret CLSs for the 12-species system from Keeling *et al.*'s measure.

For the model coral reef system, *prediction* r^2 indicates similar CLSs across multiple model runs and across physiognomic groups. However, there is more variability in *prediction* r^2 between runs for less abundant coral groups such as the acroporids (corymbose and digitate Acroporidae) and favids (Faviidae) than for turf algae. Pascual and Levin's measure indicates a CLS within the 30 – 50 cell range for all physiognomic groups. By comparison, *error X* curves very substantially between runs, and CLS interpretation using this measure is ambiguous.

In summary, both Pascual and Levin's and Keeling *et al.*'s measures (and also Rand and Wilson's measure $lVar\sqrt{X}$, which is not shown) provide unambiguous results for the simple 3-species system, but results are not so clear cut for the more complex 6- and 12-species, and coral reef systems. *Prediction* r^2 and *error X* vary between runs for these three models, with *error X* consistently more variable than *prediction* r^2.

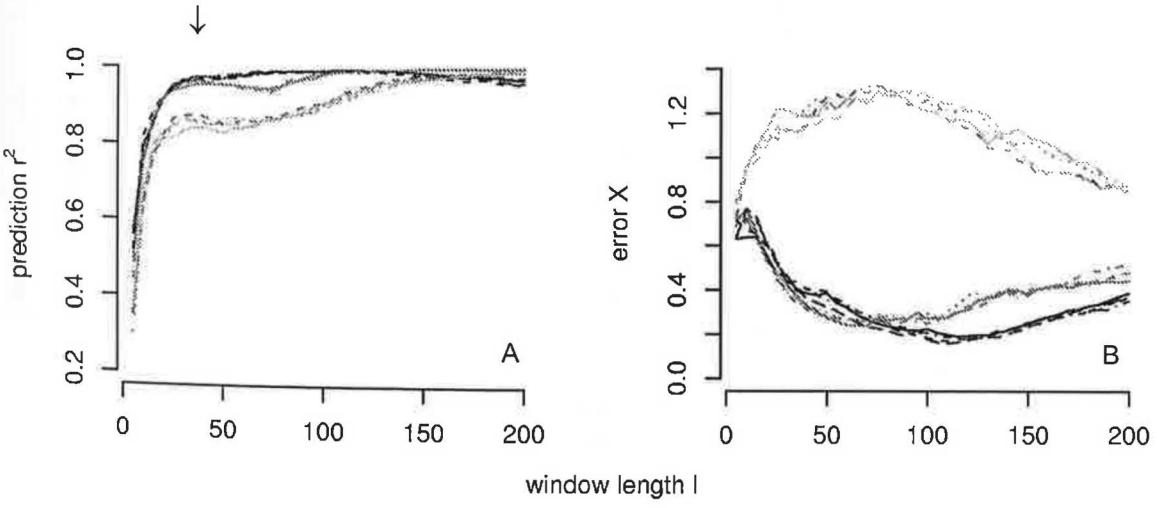


Figure 8 CLSs estimated for the 12-species system using long time series data for all species. **A** *prediction* r^2, **B** *error X*. The analysed time series contains 10000 data points sampled at each time step, with the first 200 time steps discarded. Landscape size is 500 × 500 cells. τ = 12, d_E = 6, k = 10. The arrow identifies the approximate CLS value.

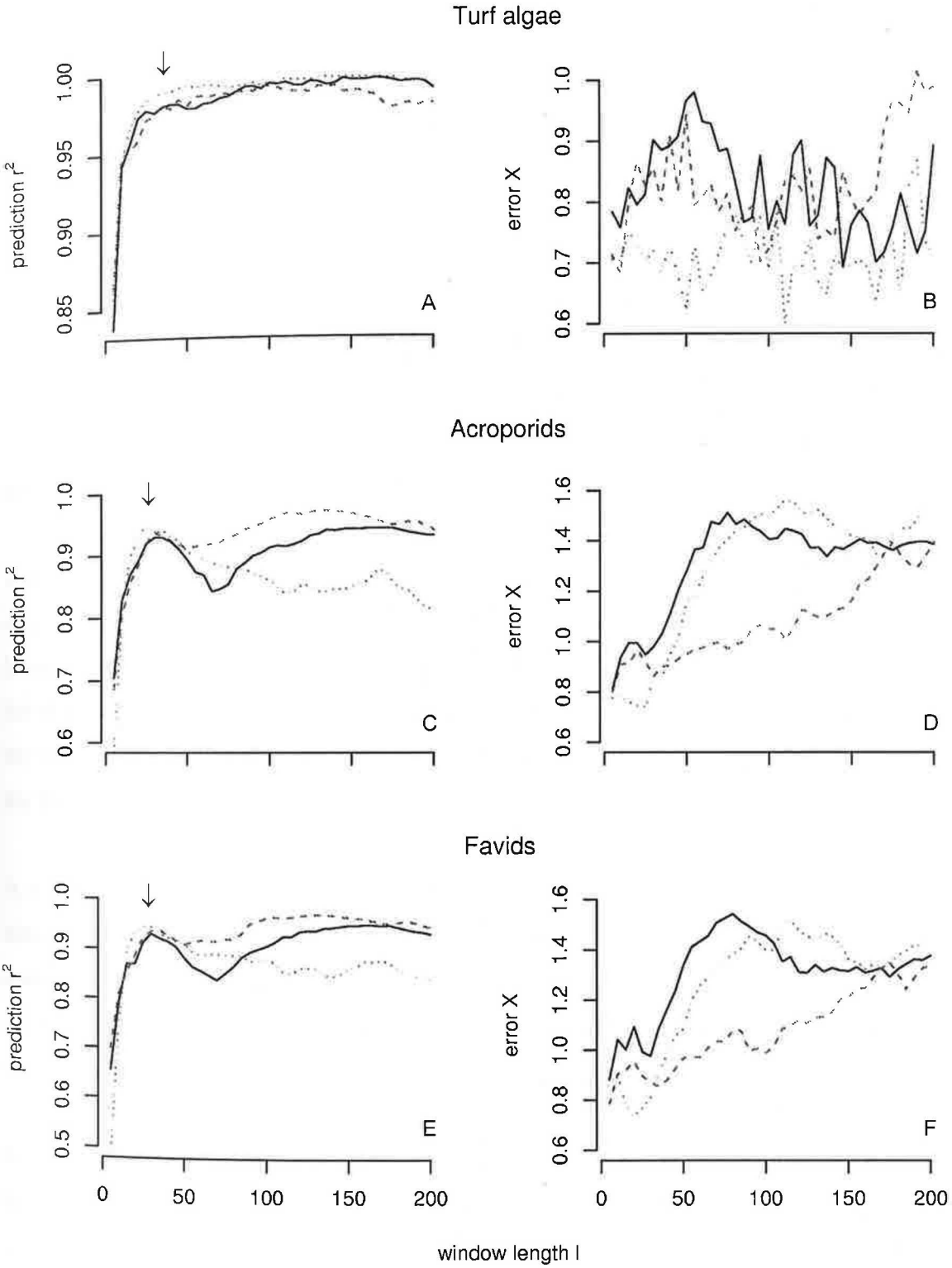


Figure 9 CLSs estimated for the coral reef system using long time series data for three physiognomic groups: turf algae (**A** & **B**), corymbose and digitate Acroporidae (**C** & **D**) and Faviidae (**E** & **F**). **A**, **C** & **E** *prediction* r^2 and **B**, **D** & **F** *error X* are presented for three model runs with different initial random configurations. Solid line = run 1, dashed line = run 2, dotted line = run 3. The analysed time series contains 10000 data points sampled at each time step, with the first 200 time steps discarded. Landscape size is 300 × 300 cells. For turf algae τ = 100, d_E = 5, acroporids τ = 75, d_E = 6 and favids τ = 100, d_E = 6. For all analyses k = 10. Arrows identify approximate CLS values.

The short time series approach

For short time series analysis, *prediction* r^2 is simpler to interpret than *error X* (Figs 10 – 12). Even so, there are slight differences in CLSs indicated by *prediction* r^2 depending on the number of embedding dimensions used for attractor reconstruction (Fig 10). Results using larger numbers of embedding dimensions (8, 9 or 10 dimensions) are not presented, but indicate similar CLSs to embeddings with 2 or 3 dimensions.

Prediction r^2 curves are similar between species within the 3-, 6- and 12-species systems and CLSs correspond with estimates from the long time series approach. There is also consistency in results from different model runs for these three systems. The CLS ranges for the 3-species, 6-species and 12-species systems inferred from *prediction* r^2 curves are 20 – 40 cells, 40 – 60 cells and 40 – 60 cells respectively (Figs 10 & 11). The relationship between CLS estimates and colony sizes for these models is examined in the final section of the results.

The short time series approach was less successful for the coral reef model. The CLS for turf algae is clearly defined between 20 – 40 cells by *prediction* r^2, however, *prediction* r^2 and *error X* are more variable between runs for less dominant coral groups (Fig 12). The reason for this variability is unclear, since changing the time step between landscapes or changing the number of landscapes used in the analysis does not reduce run-to-run variability in results for the acroporids and favids.

A notable difference between results for the 6- and 12-species systems using long time series data versus short time series data is that long time series analyses produce groupings of species and are characterised by sensitivity to initial conditions, while short time series plots are consistent between species and between model runs. It is instructive to examine these differences in greater detail.

Comparison of time series approaches

Short time series analyses for the 6-species system indicate different CLSs depending on whether data from the beginning or the end of a long time series is used (Fig 13). In Figure 13, *prediction* r^2 and *error X* curves reflect changes in the relative abundance of the six species, with one group of three species dominating after 5000 generations. In Figure 13F, the three species for which *error X* values are high are the species which dominate at the end of the time series.

Similar patterns can arise in extracting CLSs from long time series, depending on whether the system demonstrates stationary behaviour or otherwise (Fig 14). In the absence of any disturbance, the community composition of the 6-species system gradually changes, so that one group of three species becomes more numerous at the expense of the remaining three species. Such changes are more likely to occur on a small landscape (e.g. 200 × 200 cells) than on a larger landscape. This non-stationary behaviour can be stabilised and made stationary by introducing a low level of disturbance to the system, and allowing open recruitment of all species to disturbed areas with equal probability.

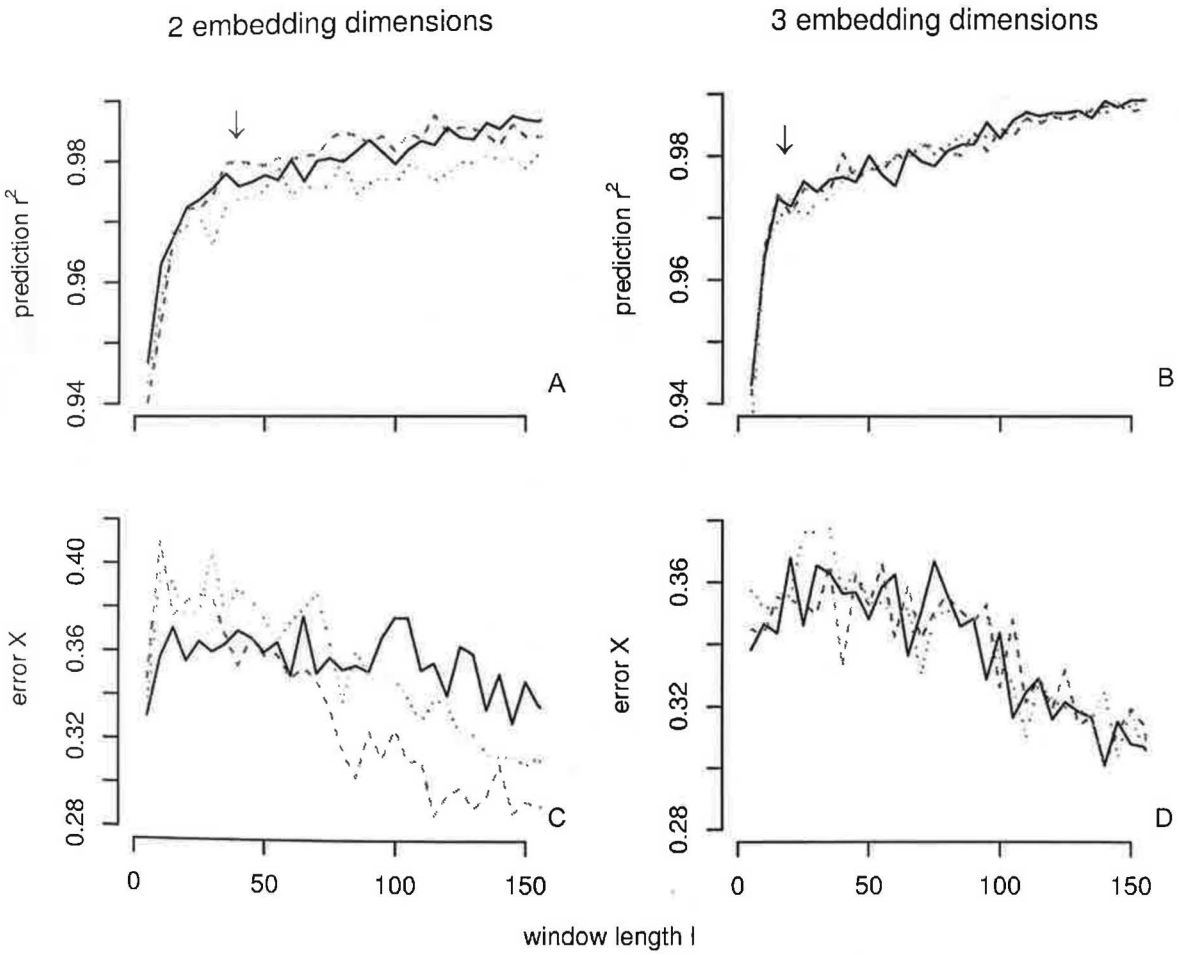


Figure 10 CLSs estimated for the 3-species system using short time series data for all species. **A** & **B** *prediction* r^2, **C** & **D** *error X*. **A** & **C** Analysed data are from landscapes 498 – 500 of 500 generations (d_E = 2). **B** & **D** Analysed data are from landscapes 497 – 500 of 500 generations (d_E = 3). Landscape size is 500 × 500 cells. τ = 1, k = 10. Arrows identify approximate CLS values.

For the non-stationary case (e.g. Fig 13A), divergence of species densities is relfected in long time series analyses. On a small landscape (200 × 200 cells), the dominant group of species shows higher values of *prediction* r^2 and lower values of *error X* (Figs 14A & 14C). Such relationships are more difficult to identify on large landscapes, where the dominance of particular three species groups changes over 10000 generations. Grouping of *prediction* r^2 and *error X* curves from long time series analysis is much less pronounced when the 6-species system is stationary (Figs 14B & 14D).

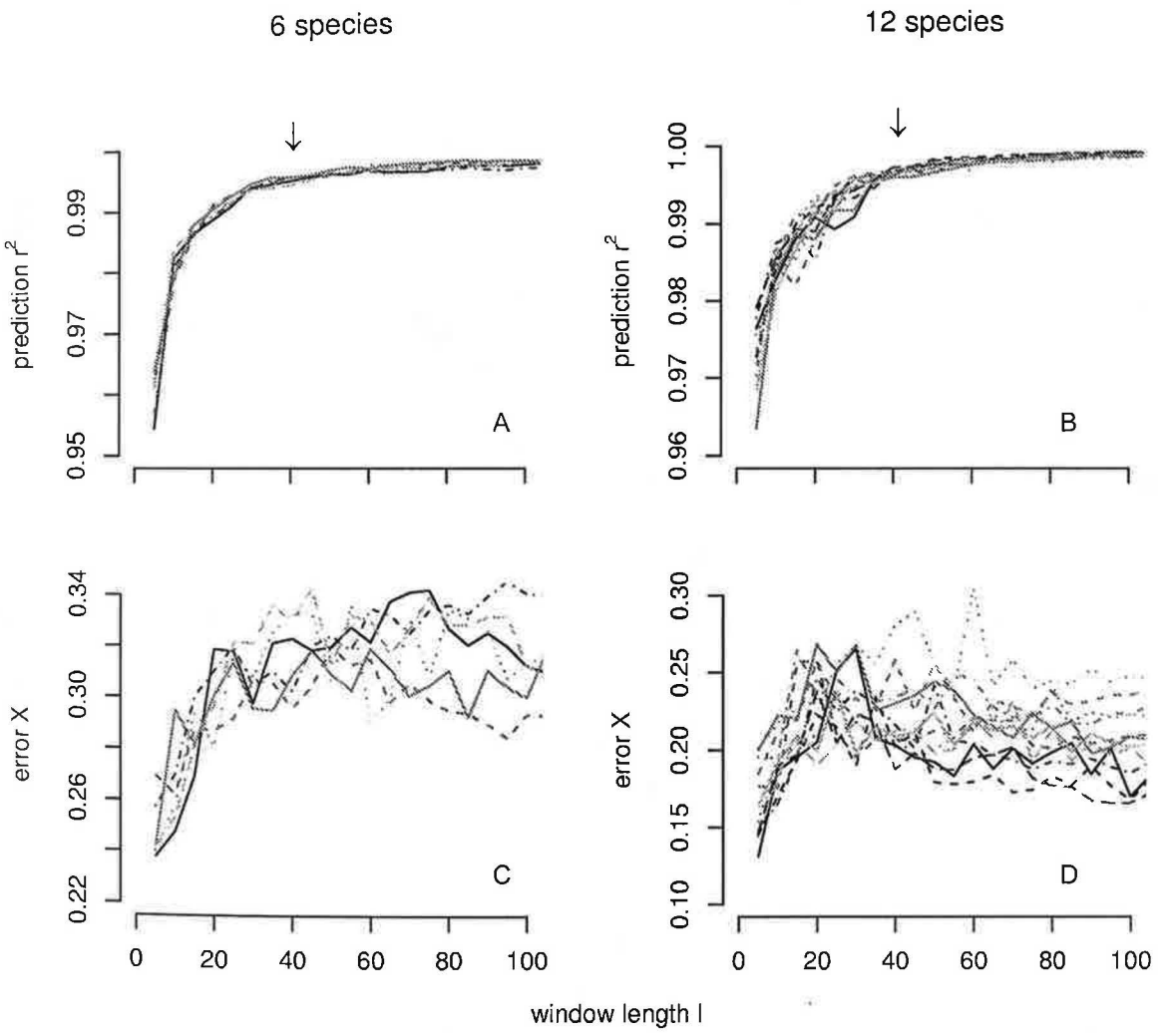


Figure 11 CLSs estimated for the 6-species (**A** & **C**) and 12-species (**B** & **D**) systems using short time series data for all species. **A** & **B** *prediction* r^2, **C** & **D** *error X*. Analysed data are from landscapes 498 – 500 of 500 generations ($d_E = 2$). Landscape size is 500 × 500 cells. $\tau = 1$, $k = 10$. Arrows indicate approximate CLS values.

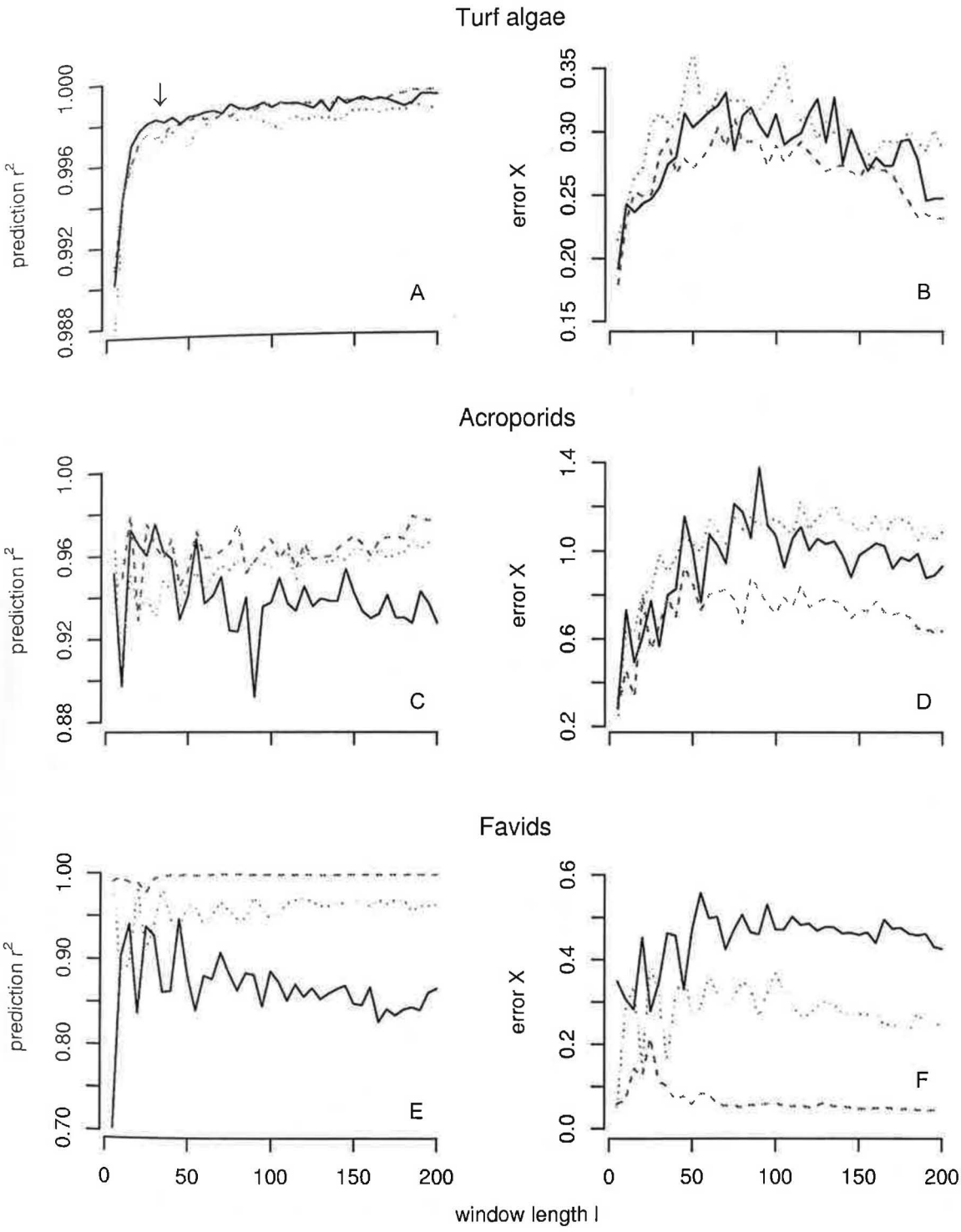


Figure 12 CLSs estimated for the coral reef system using short time series data for three physiognomic groups: turf algae (**A** & **B**), digitate and corymbose Acroporidae (**C** & **D**) and Faviidae (**E** & **F**). **A**, **C** & **E** *prediction* r^2 and **B**, **D** & **F** *error X* are presented for three model runs with different initial configurations. Solid line = run 1, dashed line = run 2, dotted line = run 3. Analysed data are from landscapes 497 – 500 of 500 generations ($d_E = 3$). Landscape size is 500 × 500 cells. $\tau = 1$, $k = 10$. The arrow identifies the approximate CLS value.

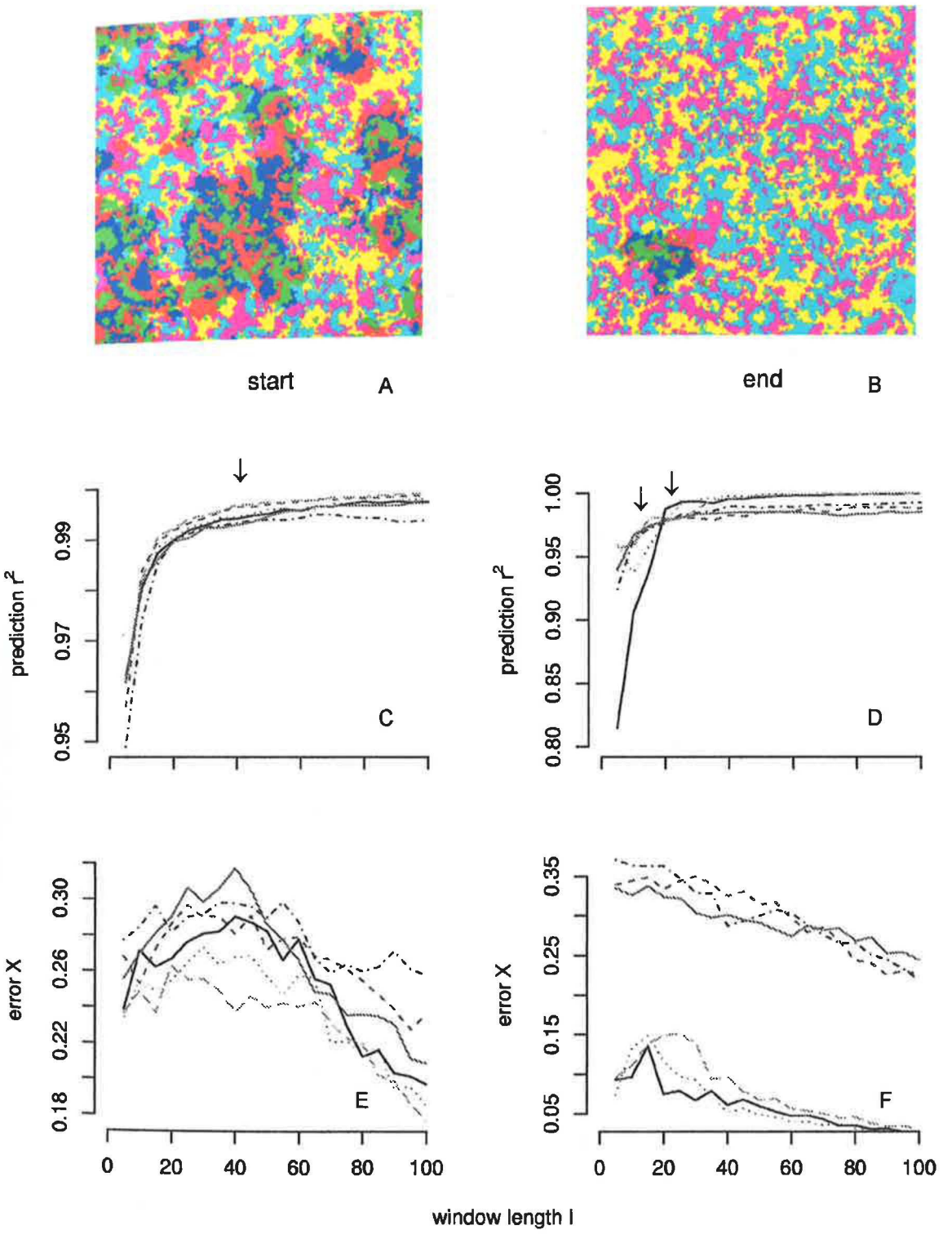


Figure 13 Short time series CLSs estimated for the 6-species system using landscapes from the start (**A**) and the end (**B**) of a 5000-generation time series. **C** & **D** *prediction* r^2, and **E** & **F** *error X* are presented for all six species. Analysed data are from four landscapes: generations 1 – 4 (**C** & **E**) and generations 4997 – 5000 (**D** & **F**). Landscape size is 200 × 200 cells. $\tau = 1$, $d_E = 3$, $k = 10$. Arrows identify approximate CLS values. Divergence in species abundances is reflected in the grouping of *prediction* r^2 and *error X* curves in **D** & **F**.

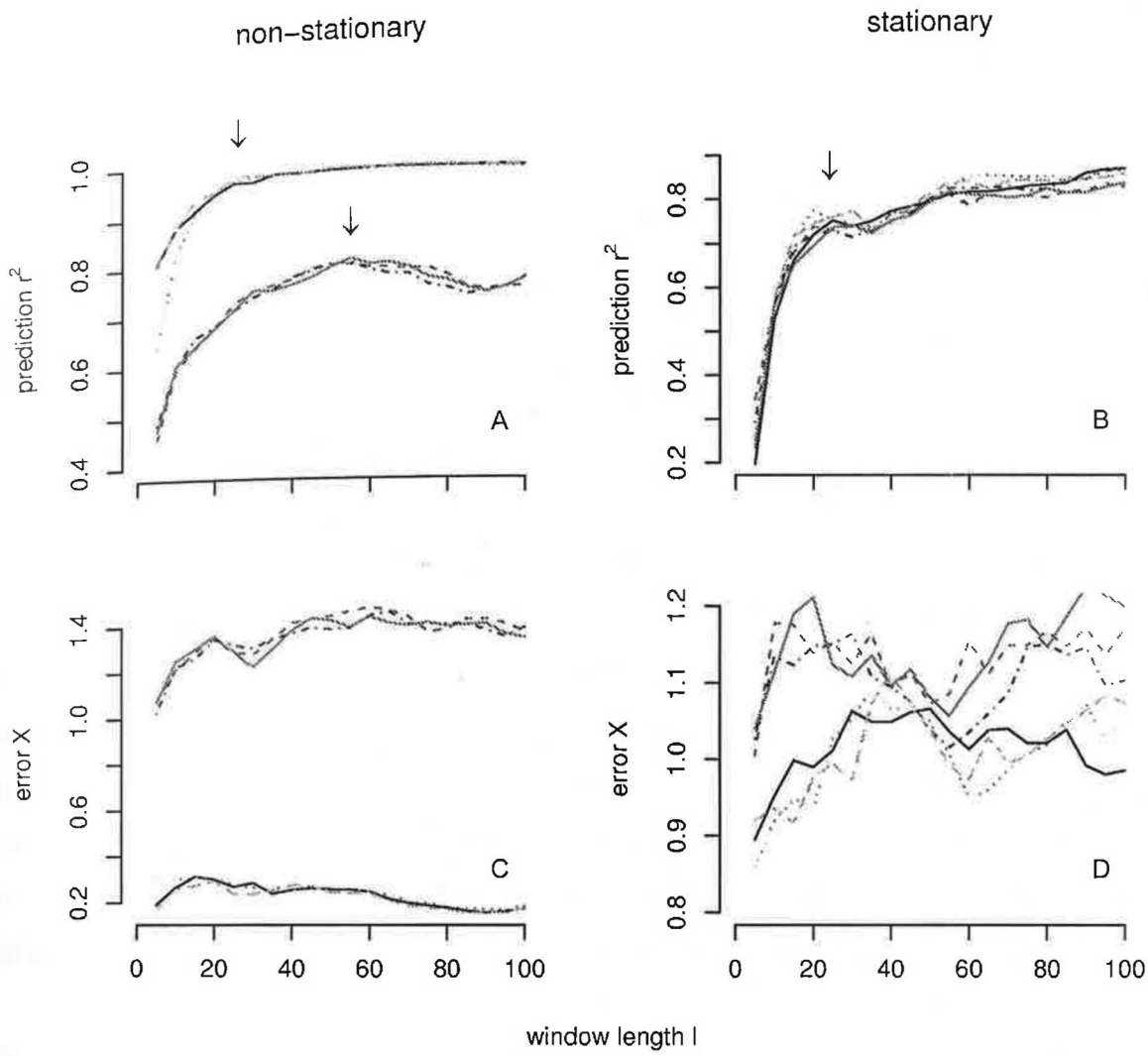


Figure 14 CLSs estimated for the 6-species system using long time series data for all species. Analysed data are from **A** & **C** a non-stationary system and **B** & **D** a stationary system (see text for explanation). **A** & **B** *prediction* r^2, **C** & **D** *error X*. The analysed time series contains 5000 data points, sampled at each time step. Landscape size is 200 × 200 cells. For **A** & **C** τ = 12, **B** & **D** τ = 19. In all cases d_E = 6, k = 10. Arrows identify approximate CLS values.

Sliding windows

In the sliding window approach to attractor reconstruction, the units of the embedding delay τ are cells rather than time steps. This means that, for a fixed delay of n cells, there is greater overlap of successive dimensions for large windows than for small windows. The problem of different degrees of overlap should not arise if the embedding delay is some proportion of the linear dimensions of the window. Therefore, the first step in developing the sliding window method is to compare the performance of fixed delays versus delays which are proportional to the window length.

Evaluation of fixed and proportional delays

Randomly generated landscapes of independent, discrete valued pixels provide a null case to evaluate fixed and proportional delays. The expected result of long time series analyses using independent, random landscapes is constant *prediction* r^2 and *error X*, i.e. level curves for both CLS measures (see Appendix for proof and empirical verification). The probability, Π, of observing pixels with a particular discrete value can be adjusted so that this null case is the randomised equivalent of an *n*-species system. For example, $\Pi = 0.3$ (Fig 15) provides the (approximate) randomised equivalent of a 3-species system.

Prediction r^2 and *error X* curves for sliding window analyses of random landscapes are not constant when the embedding delay is fixed, $\tau = 10$ (Fig 15A &15B). Such *prediction* r^2 and *error X* curves might instead be expected for a system with defined spatial patterns. Qualitatively similar results are obtained from other integer values of τ ($1 \leq \tau \leq 10$). By comparison, trends in *prediction* r^2 and *error X* curves are reduced (Figs 15C & 15D) or absent (Figs 15E & 15F) when delays proportional to window length are used in attractor reconstruction. The reason for discrepancies in results for $\tau = 0.8 \times$ window length and $\tau = 0.1 \times$ window length is unclear. Nevertheless, proportional delays are preferable to fixed delays for sliding window embeddings and so are used in the following analyses.

Sliding window results for model systems

The first minimum on scaled mutual information versus τ curves was at $\tau = 0.8 \times$ window length for all four model systems, suggesting that this is the most appropriate embedding delay for attractor reconstruction. However, sliding window analyses for the 3-species system indicate that CLS estimates change depending on the proportion chosen for τ (Fig 16). Estimated CLS ranges increase from 20 – 40 cells to 50 – 70 cells when the delay changes from $\tau = 0.8 \times$ window length to $\tau = 0.2 \times$ window length. Similarly for the 6- and 12-species systems, the observed increase in CLS range was from 40 – 60 cells to 140 – 150 cells. The reason for this dependence on τ is unclear.

Despite sensitivity of *prediction* r^2 and *error X* curves to the value of τ, CLSs estimated from sliding window analyses (with $\tau = 0.8 \times$ window length) correspond with time series CLSs for the four model systems. CLSs from the three approaches are compared in more detail in the final section of the results. *Prediction* r^2 and *error X* are generally consistent between model

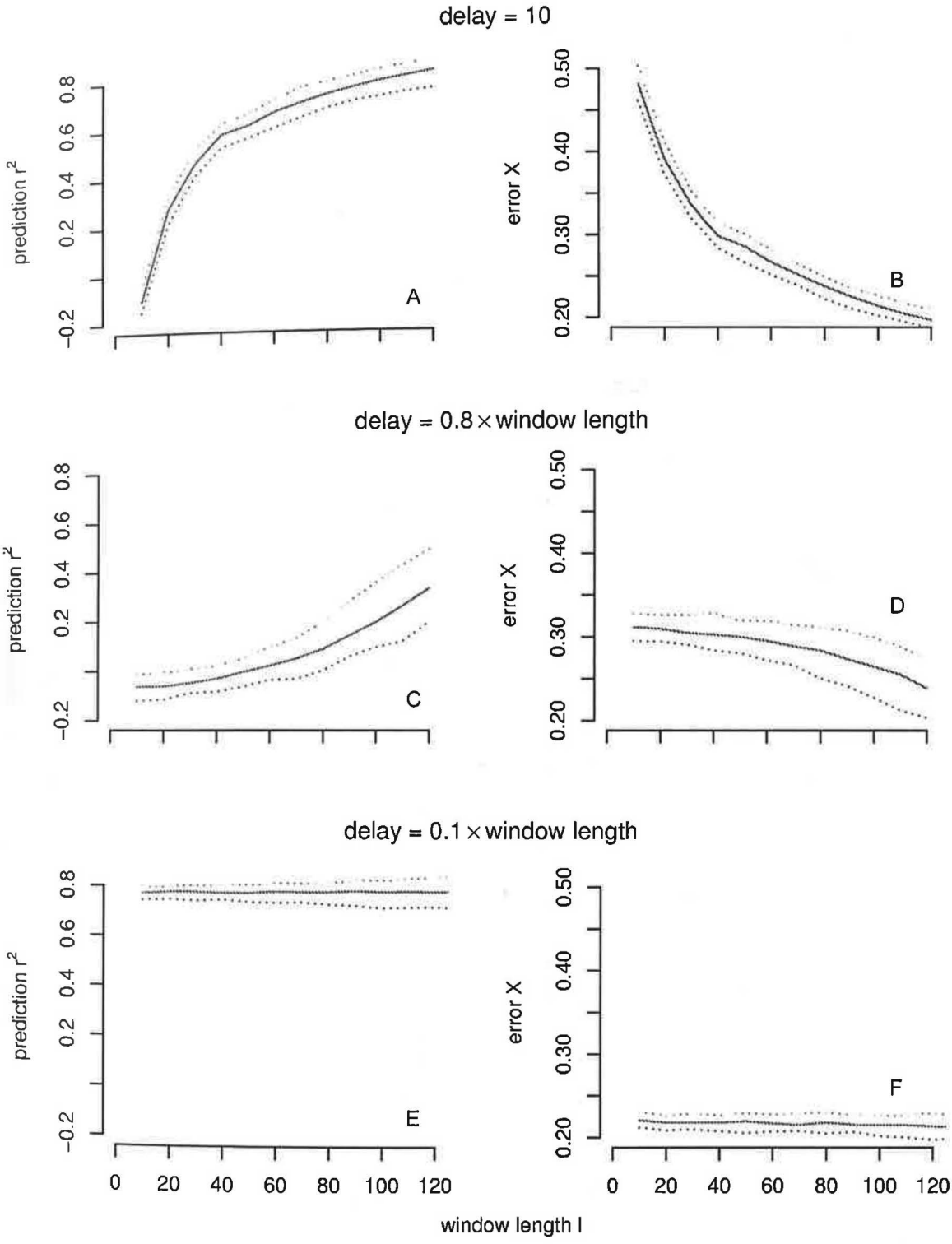


Figure 15 **A**, **C** & **E** *prediction* r^2 and **B**, **D** & **F** *error X* curves for sliding window analyses using simulated frames of independent, discrete valued pixels. In simulated frames, the probability of observing pixels with a particular discrete value is $\Pi = 0.3$. **A** & **B** $\tau = 10$, **C** & **D** $\tau = 0.8 \times$ window length, **E** & **F** $\tau = 0.1 \times$ window length. For all plots $d_E = 5$. Landscape size is 700 × 700 pixels. Solid lines indicate average curves for 100 replications and dotted lines indicate 95% confidence intervals.

runs and across species within a system using the sliding window approach. In the coral reef model the Faviidae (which occur in small patches of approximately 10 × 10 cells) show the greatest variability between model runs. However, all physiognomic groups in the coral reef model indicate a similar CLS range of 30 – 50 cells.

A surprising aspect of sliding window results is that Keeling *et al.*'s measure *error X* is more interpretable than Pascual and Levin's *prediction* r^2 for all four model systems. While the inflection in *prediction* r^2 curves is unambiguous, it generally occurs at a smaller scale than inflection in *error X* curves. It is unclear why *prediction* r^2 curves are inverted from the time series case.

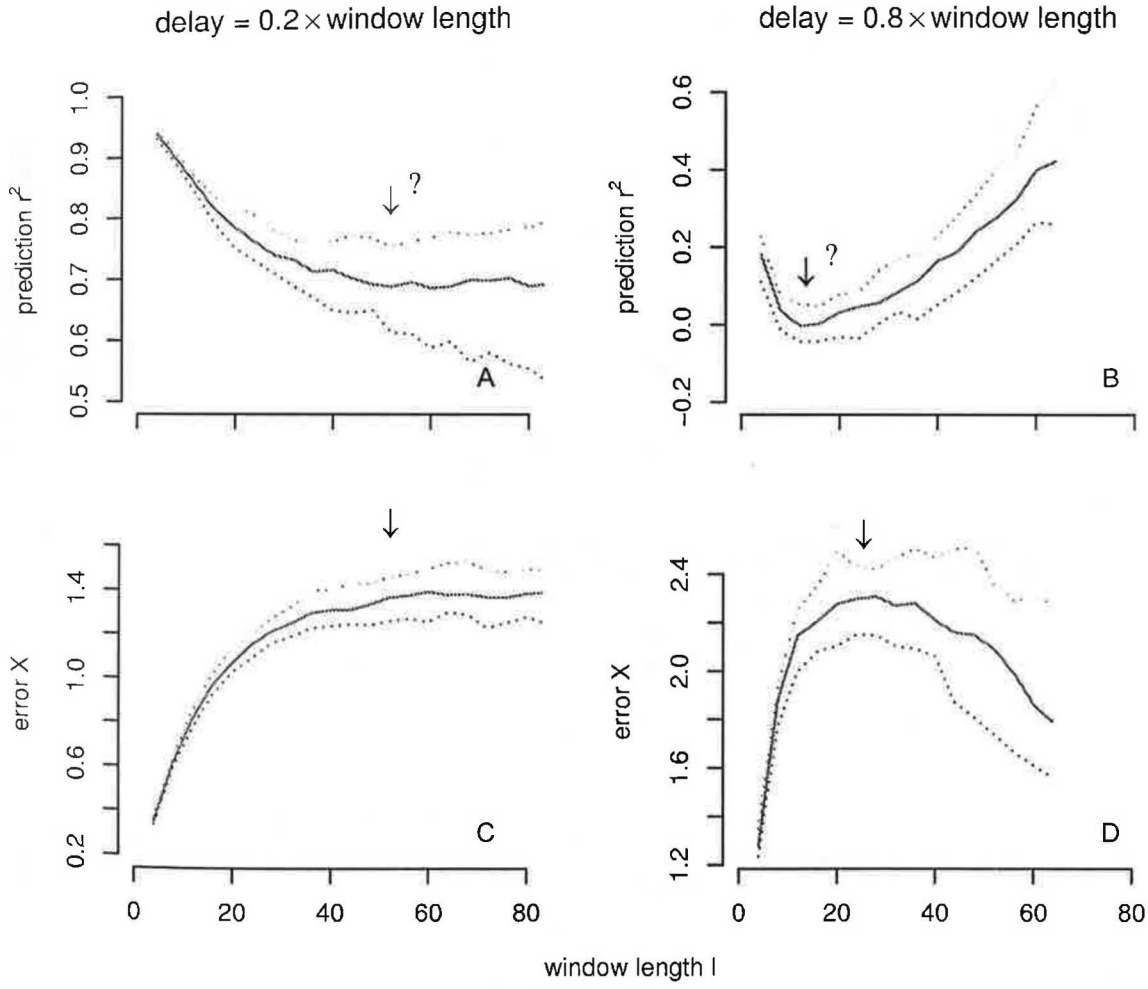


Figure 16 CLSs estimated for the 3-species system using sliding window analysis. **A** & **C** *prediction* r^2 and **B** & **D** *error X* curves are presented for species 1. Landscape size is 500 × 500 cells. For **A** & **B** τ = 0.2 × window length, d_E = 4, k = 10 and for **C** & **D** τ = 0.8 × window length, d_E = 5, k = 10. Solid lines indicate average curves for 50 model runs and dotted lines indicate 95% confidence intervals. Arrows identify approximate CLS values, and question-marked arrows identify inflections. Confidence intervals confirm that the shapes of curves are reasonably consistent between model runs.

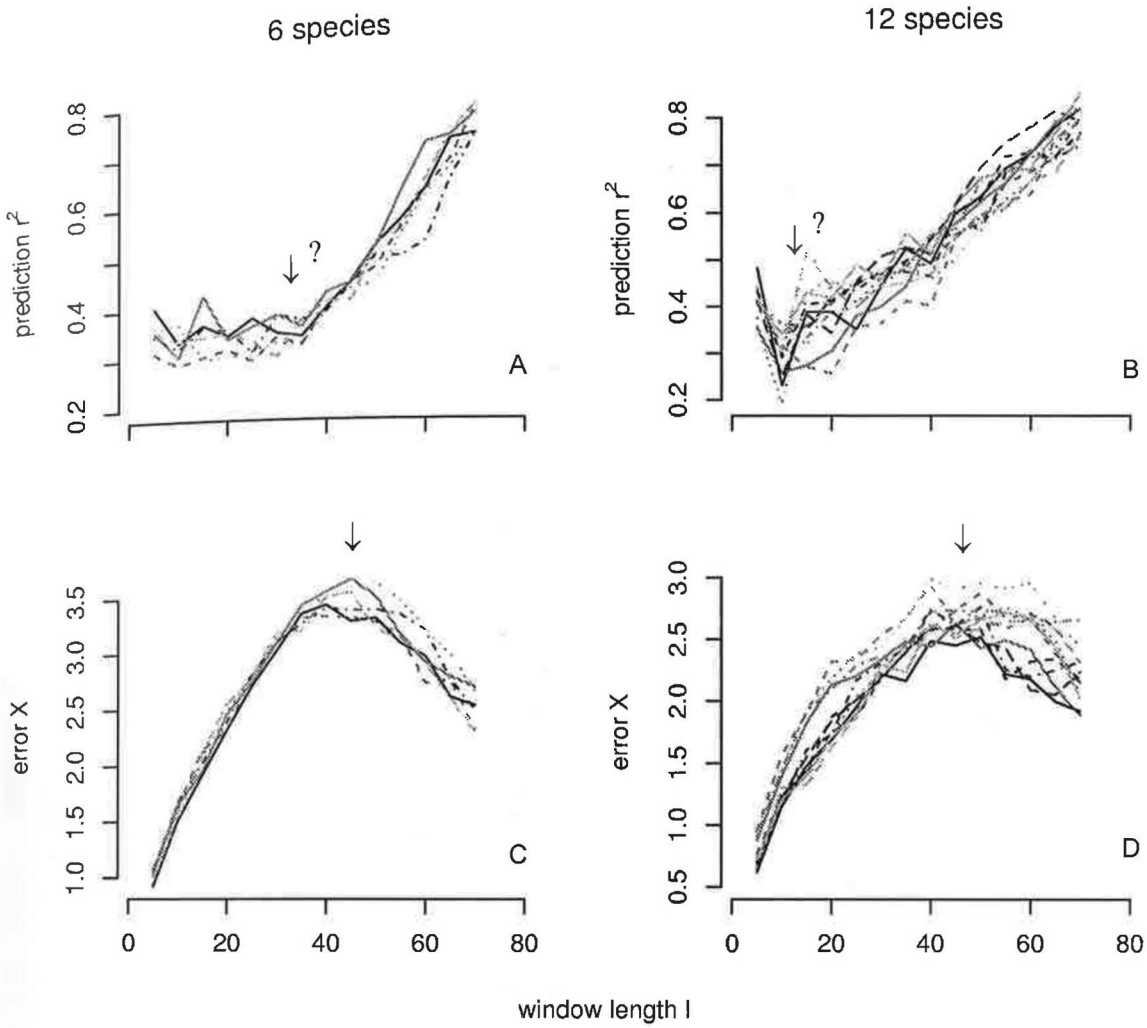


Figure 17 CLSs estimated for **A** & **C** the 6-species system and **B** & **D** the 12-species system using the sliding window approach. **A** & **B** *prediction* r^2 and **C** & **D** *error X* curves are presented for all species. Landscape size is 500 × 500 cells. τ = 0.8 × window length, d_E = 6, k = 10. Arrows identify approximate CLS values, and question-marked arrows identify inflections.

Variograms and nested ANOVA

The scale at which variograms asymptote to a constant value indicates the scale of spatial pattern in the analysed data. The asymptotic scale for variograms in Figure 19 is 20 cells for the 3-species system and 60 cells for the 6-species and 12-species systems. Notably, variogram analyses did not detect the two scales of spatial pattern formation in the 6- and 12-secies systems (i.e. small-scale colonies and large-scale multi-species patches). For the coral reef system, scales of spatial pattern indicated by variograms in Figure 19 are smaller for acroporid and favid corals (20 cells and 10 cells respectively) than for turf algae (40 cells).

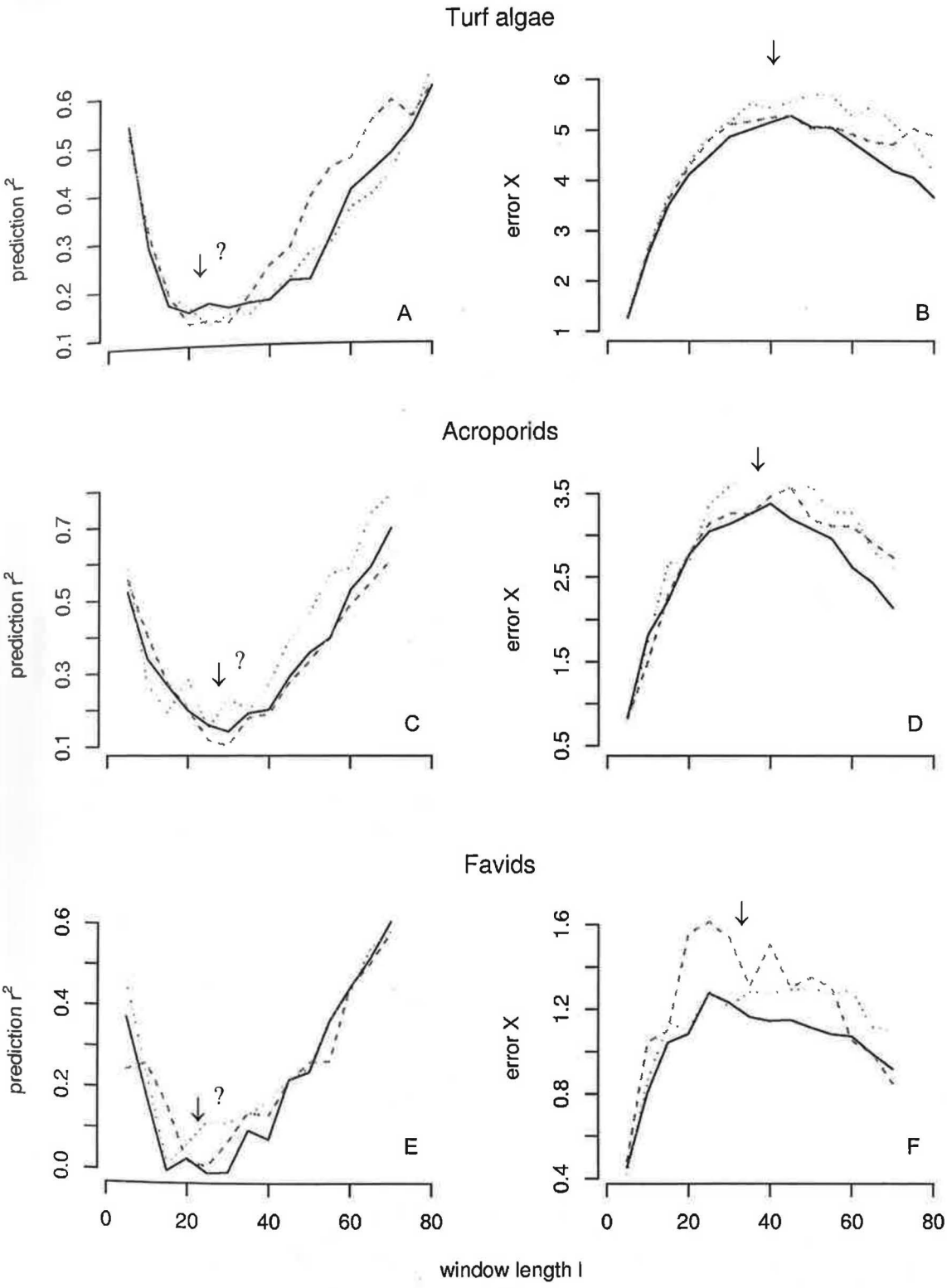


Figure 18 CLSs estimated for the coral reef system using sliding window data for three physiognomic groups: turf algae (**A** & **B**), corymbose and digitate Acroporidae (**C** & **D**) and Faviidae (**E** & **F**). **A**, **C** & **E** *prediction* r^2, **B**, **D** & **F** *error X* are presented for three model runs with different initial random configurations. Solid line = run 1, dashed line = run 2, dotted line = run 3. Landscape size is 500 × 500 cells. For all plots $\tau = 0.8 \times$ window length, $k = 10$. **A** $d_E = 5$, **B** & **C** $d_E = 6$. Arrows identify approximate CLS values, and question-marked arrows identify ambiguous inflections.

The scales of spatial pattern indicated by variograms for the 3-species and coral reef systems correspond with colony sizes in the model. For the 6 and 12-species systems, the scales indicated are intermediate between the colony size and the larger scale of multi-species patches.

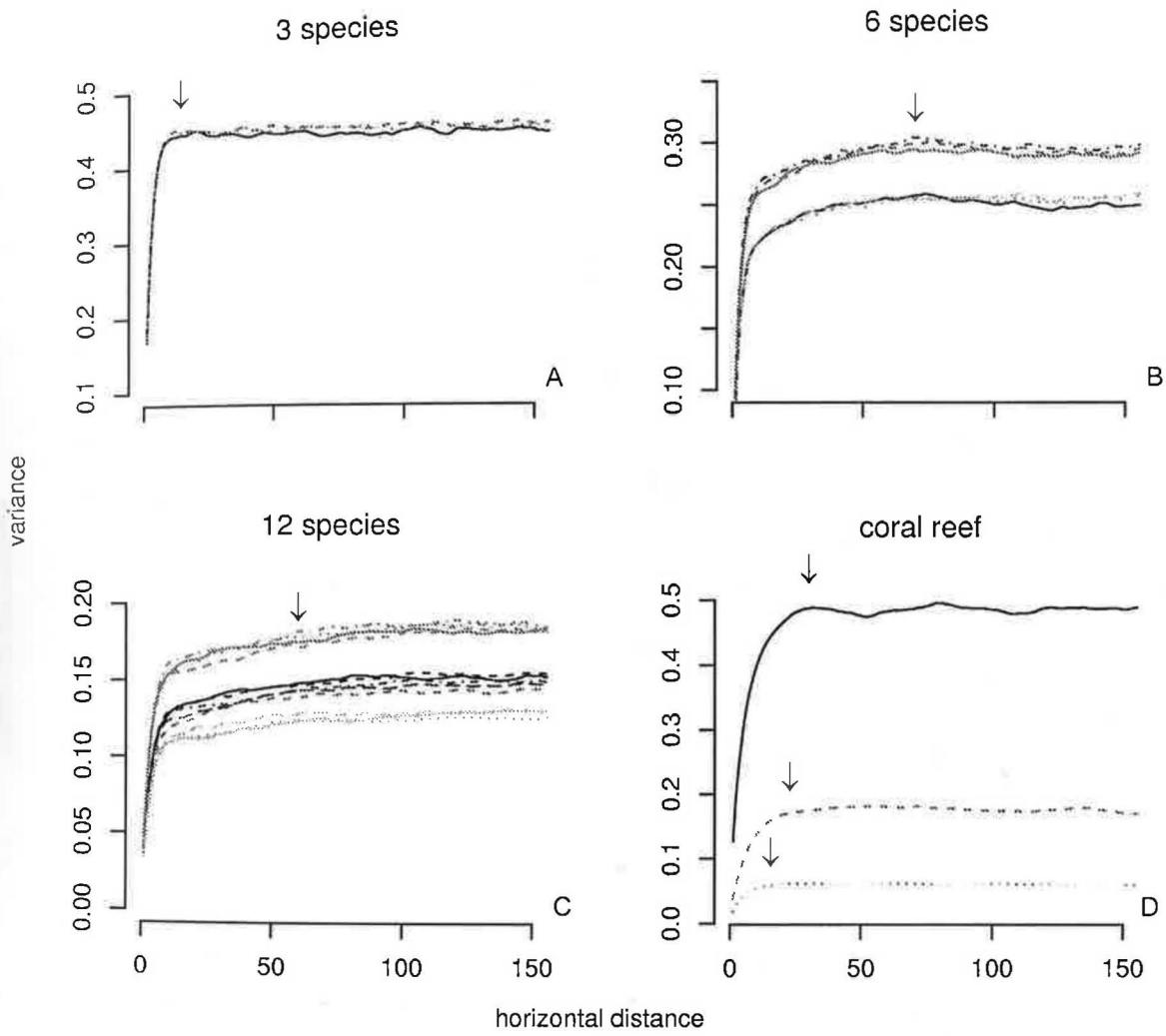


Figure 19 Variance versus horizontal distance for the four model systems (variograms using vertical distances were identical). Curves for all species are shown for the **A** 3-species, **B** 6-species and **C** 12-species systems. **D** Curves for three physiognomic groups in the coral reef system are presented: turf algae (solid line), digitate and corymbose Acroporidae (dashed line) and Faviidae (dotted line). Landscape size is 500 × 500 cells. Landscapes are sampled at the 500th generation. Arrows identify the approximate scale at which variograms plateau – the scale of spatial pattern in the analysed data.

Nested ANOVA of hierarchically sampled spatial data indicates that, in all but the coral reef system, more than half of the variance is attributable to the smallest scale or the error level. In all four model systems the effect of small scales was significant while large scales did not have a significant effect on density. The spatial scale at which variance plateaus is approximately 30 cells for the 3-species system, 150 cells for the 6-species and 12-species systems and 90 cells for the coral reef system (Fig 20).

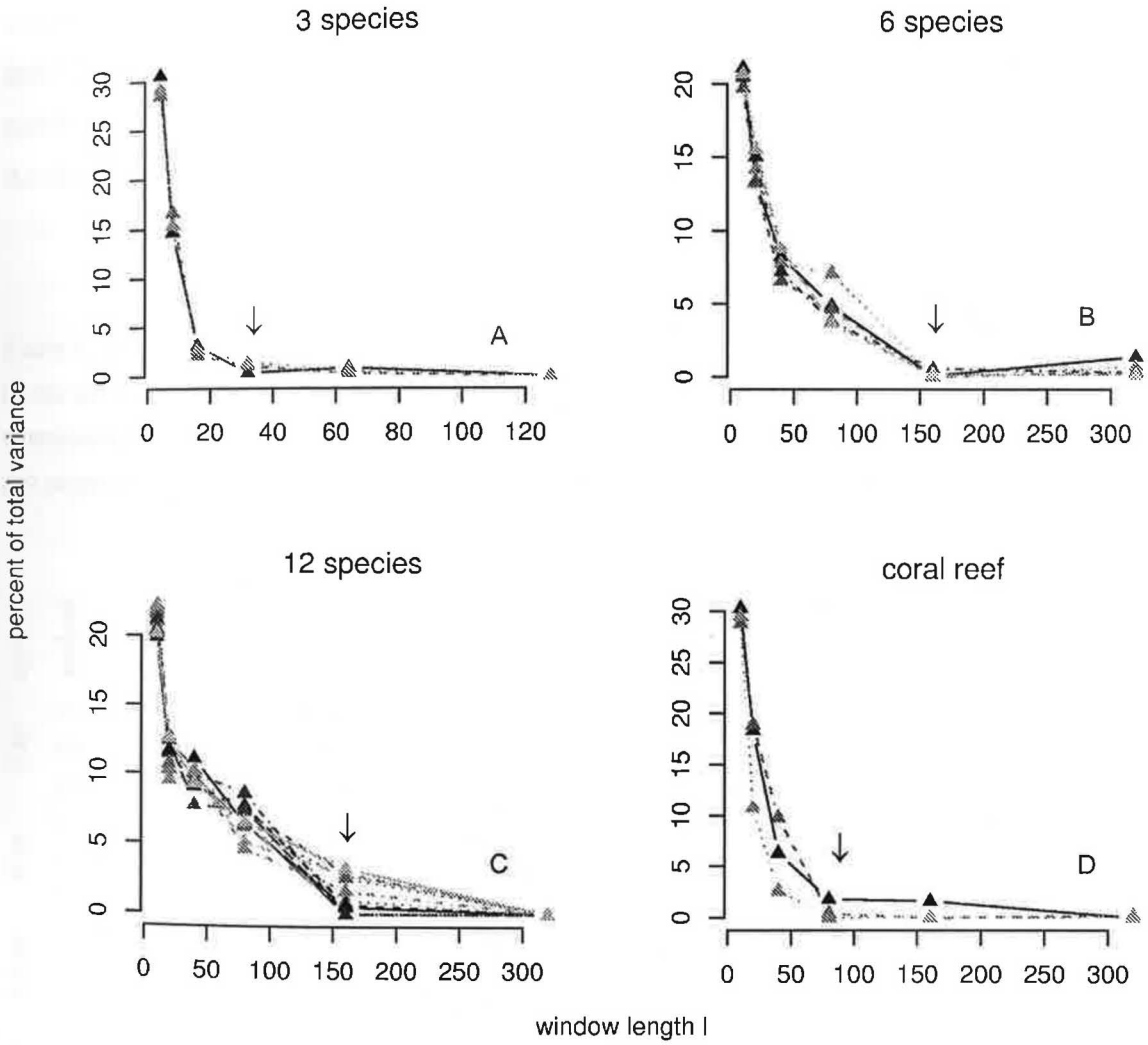


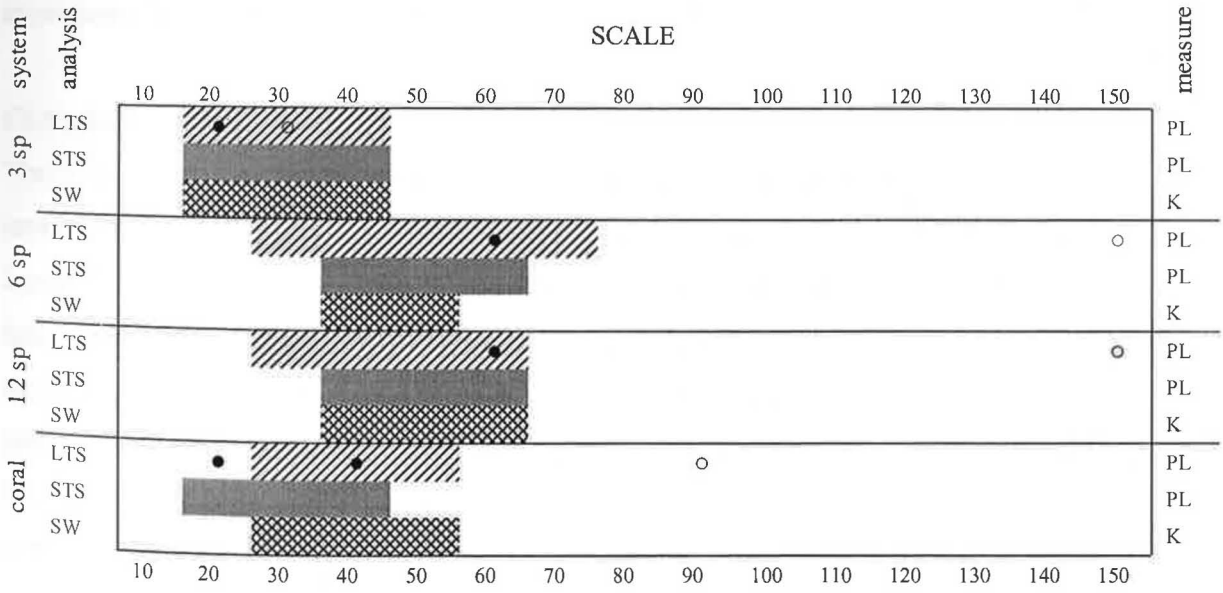
Figure 20 Percent contribution to variance versus spatial scale, with values calculated from nested ANOVA of hierarchically sampled spatial data. Curves for all species are shown for the **A** 3-species, **B** 6-species and **C** 12-species systems. **D** Curves for three physiognomic groups in the coral reef system are presented: turf algae (solid line), digitate and corymbose Acroporidae (dashed line) and Faviidae (dotted line). Landscape size is 500 × 500 cells. Landscapes are sampled at the 500th generation. Arrows indicate the spatial scale at which variance plateaus.

CLS summary

CLS estimates from the three different techniques of attractor reconstruction (i.e. long time series, short time series and sliding windows) generally correspond for each model system (Table 1). While variogram analyses indicate spatial scales which lie close to or within CLS ranges, results from nested ANOVA suggest much larger scales of spatial pattern.

CLS ranges for the 6- and 12-species systems are almost identical, and are consistently larger than those for the 3-species system. The CLS of 20 – 40 cells for the 3-species system is slightly larger than the approximate colony size in this model of 10 – 20 cells. CLSs for the 6- and 12-species systems are intermediate between colony size and the size of multi-species patches. For the coral reef model, CLSs are slightly smaller than the scale of colony sizes for the dominant turf and coralline algae.

Table 1. Summary of CLSs from long time series, short time series and sliding window analyses. CLSs were estimated using *prediction* r^2 or *error X* – whichever measure gave the clearest interpretation. Spatial scales indicated by variograms and nested ANOVA are also included. Results are presented for the 3-species, 6-species, 12-species and coral reef systems.



● = scale of pattern indicated using variograms

○ = scale of pattern from nested ANOVA

LTS = Long Time Series; STS = Short Time Series; SW = Sliding Window

PL = estimate from *prediction* r^2 (Pascual and Levin 1999)

K = estimate from *error X* (Keeling *et al.* 1997)

DISCUSSION

The search for techniques to identify robust and meaningful length scales in ecological systems has a long history. This effort has been sustained in recent times given the pressing need for objective means to identify appropriate scales for management units (Garcia-Charton and Perez-Rufaza 1999), conservation areas (Castilla 2000), and the detection of meaningful trends in system dynamics (Underwood and Chapman 1998). The recently developed techniques of Keeling *et al.* (1997) and Pascual and Levin (1999) for estimating CLSs are attractive because they adopt non-linear time series techniques to accommodate complex oscillatory behaviour. However, as they currently stand, these analyses require long time series of data which cannot realistically be collected for most natural systems.

This thesis describes two alternative approaches to sampling data in dynamical systems that have considerable potential for overcoming the data requirement problem of Keeling *et al.*'s (1997) and Pascual and Levin's (1999) techniques. The short time series approach requires only three or four consecutive landscapes to estimate CLSs while the sliding window method requires spatial data from just a single point in time. Results suggest that, in addition to unrealistic data requirements, the long time series measures developed by Keeling *et al.* (1997) and Pascual and Levin (1999) are inadequate for at least some model systems that are more complex than the simple 3-species case.

CLSs from long time series

The 3-species system in this study is similar to model systems used previously for investigating CLSs (Rand 1994, Rand and Wilson 1995, Keeling *et al.* 1997, Pascual and Levin 1999, Wilson and Keeling 2000) in that it self-organises at only one spatial scale and has a limited number of species. CLSs from long time series data can be identified unambiguously for the 3-species system, and are consistent between model runs with different initial random configurations and between different species in the system. Pascual and Levin's (1999) *prediction* r^2 reaches its asymptote at a smaller scale than Keeling *et al.*'s (1997) *error X*, supporting Pascual and Levin's (1999) argument that the scale of maximum determinism can be below the scale at which windows are independent (i.e. where $1/l^2$ scaling occurs).

Prediction r^2 and *error X* curves for long time series data from the 6- and 12-species systems and the coral reef system are more difficult to interpret than those obtained for the 3-species system and for other published simple model systems. There are several important differences between these three former models and those models used in previous investigations of CLSs. Prior studies have analysed data from systems with a maximum of four species, and results have been presented for only a single species in any particular model. Another difference is that the 6- and 12-species systems used here exhibit self-organisation at more than one spatial scale. Finally, the coral reef system behaves similarly to the real system from which it has been parameterised and lacks the well defined periodic oscillations present in the dynamics of most previously examined models.

Asymptotic points were better defined for *prediction* r^2 than for *error X* in long time series analysis of the 6-, 12- and coral reef systems. However, both measures demonstrated substantial run-to-run variability, particularly for the 6- and 12-species systems. Marked differences in the shape of *error X* and *prediction* r^2 curves between runs in long time series analyses could not be related to the dynamics of individual runs. This variation may be attributable to non-stationarity on long time scales.

When landscapes are small (for example 200 × 200 cells) and in the absence of continuous open recruitment to the landscape, the 6- and 12-species systems are non-stationary over 10000 generations. One group of three species in the 6-species system, or one group of four species in the 12-species system dominates by the end of the time series. Although larger landscapes (500 × 500 cells) are stationary in the sense that one group of species does not become dominant over 10000 generations, time series data may not be stationary at small sampling scales (window sizes). This effect is exaggerated since window sampling is at a fixed position on the landscape. Sampling at a fixed point ignores variability over the landscape and is a disadvantage of the long time series method compared with the sliding window and short time series approaches, both of which sample the whole landscape.

Extreme occurrence of non-stationarity may involve a transition between attractors over a long time series. This is not necessarily a problem for model systems, but may occur commonly in the real world. Solé and Bascompte (1995) point out that planktonic systems are a particular example in which transition between different attractors is likely over a long time

series, because these systems are interrupted by external inputs of energy. Long time series analysis is inappropriate for cases where there is transition between attractors.

Prediction r^2 was more consistent from run to run in the coral reef system than for the 6- and 12-species systems. In the coral reef modal, relative densities of the twelve physiognomic groups change over 10000 generations, but turf and coralline algae are always the dominant space occupants. Landscapes from this system are more spatially homogenous than landscapes from the 6- and 12-species systems that vary in their spatial arrangement of multi-species patches. Essentially stationary dynamics and landscape homogeneity are explanations for the consistency of *prediction* r^2 curves between runs, however, the reason for ambiguities in *error X* results for this system is unclear.

CLSs from sliding windows

The sliding window approach to attractor reconstruction is the most extreme alternative to estimating CLSs from long time series. If successful, the sliding window technique would enable estimation of CLSs from spatial data obtained at a single sampling occasion. However, replacing temporal variability with spatial variability complicates non-linear time series analysis. In particular, results of this thesis indicate that sliding window analysis requires embedding delays that are proportional to window size rather than delays of a fixed number of cells. Proportional delays ensure that the overlap of successive embedding coordinates is constant for all window sizes.

CLSs estimated using *error X* curves from sliding window analyses are similar to the estimates obtained from analysis of long time series. However, the former estimates are very sensitive to the value of the proportional delay used for attractor reconstruction. There is no clear explanation for this sensitivity. Also unclear is the cause of observed inversions in the shapes of *prediction* r^2 and *error X* curves for sliding window analyses.

A further shortcoming of the sliding window approach is that the maximum window size which can be sampled on a given landscape size is limited. Depending on the value of the delay, the maximum window size may be significantly smaller than the landscape. If the CLS for the system is below the landscape scale, but above the scale of the maximum window size then it will not be detected. This problem does not arise in either of the two time series

approaches, where windows up to and including the landscape scale can potentially be analysed.

Evaluation of the observed results for sliding window analyses requires mathematical consideration beyond the scope of this thesis. Such inquiries are nonetheless important, since information from the spatial dynamic of a system is equally legitimate to the temporal signal for defining a CLS. Spatial and temporal signals in ecology are closely related: temporal dynamics are strongly influenced by spatial arrangements, and similarly, information about temporal dynamics is contained in spatial data (Solé and Bascompte 1995). We would therefore expect CLSs determined using the sliding window sampling method to complement time series CLSs estimates, and the spatial approach should not be dismissed.

An achievable intermediate: short time series

The short time series method integrates sampling through time, but on few occasions, with spatial sampling as in the sliding window technique. The use of short time series for estimating CLSs has the combined advantages of sampling the entire landscape at each time step, while still using time series variability as the basis for CLS estimates. With regard to the principal aim of this work, the requirement for three or four sampling occasions is realistic for many applications in ecology and so the approach is promising.

A further advantage of using information from only a small number of time steps is that ecological systems are likely to be essentially stationary over the sampling period. As results for the 6- and 12-species systems indicate, non-stationarity over long time scales produces *prediction* r^2 and *error X* curves that are difficult to interpret. The corresponding curves generated from short time series analysis are, by comparison, readily interpretable. Short time series CLSs from the beginning and the end of a long non-stationary time series clearly reflect changes in the state of the system. Thus, the short time series technique could potentially be used to detect trends in natural systems as changes in the CLS. Applied examples may include determining whether a pollutant or the introduction of a foreign species changes the state of an ecological system.

Results from Pascual and Levin's (1999) *prediction* r^2 were generally easier to interpret than Keeling *et al.*'s (1997) *error X*, for data derived from short time series. However, *prediction* r^2 and *error X* spectra developed for two coral groups (corymbose and digitate Acroporidae

and Faviidae) in the coral reef model varied between model runs and the definition of CLSs from these results was ambiguous. A potential explanation for this variability is that the number of landscapes used for attractor reconstruction, and/or the time step between landscapes are insufficient to capture the important dynamic signal for these corals, and hence to determine the CLS. Since acroporid and favid corals occur in small patches, a longer time period may be required to derive a reliable estimate of the ratio of deterministic signal to noise in the dynamics of these groups. However, this explanation is not supported by investigation of the effects of altering the time step between data points and of using more time steps, given that these changes produced similarly ambiguous results for the coral reef model.

Investigations for the 3-, 6-, and 12-species systems using a range of values for τ (the time step between landscapes) and d_E (the number of landscapes) suggest that CLSs estimated using short time series are robust to these parameters. It is likely that the short time series approach will be generally robust to embedding parameters, provided the data set is stationary over the sampling period. As such, the short time series approach is a promising method for estimating CLSs and has reasonable data requirements for ecological applications.

Performance of conventional spatial methods

Scales of spatial pattern determined using conventional analysis techniques provide an interesting comparison with scales of 'maximum non-trivial determinism' (CLSs). Of the two static spatial measures compared in this thesis, variograms provide a more interesting interpretation for the four model systems, than does nested ANOVA. Variograms indicate spatial scales that correspond approximately with CLS estimates, while nested ANOVA suggests plateaus in variability at much larger scales.

The asymptotic scales of variograms generated for the 3-species and coral reef systems reflect the colony sizes of individual species in these models. For the 6- and 12-species models, however, variogram analysis failed to distinguish the two scales of spatial pattern – individual colonies and multi-species patches. The most likely explanation is that variograms are limited to the detection of exact spacings on a landscape. Variograms are therefore useful to detect the scale of colony formation (because colony size is relatively consistent), but not in detecting the scale of grouping of colonies of several species in the 6- and 12- species systems (because clumps of associated species are so variable in size).

In the coral reef model, variogram analysis detected differences in colony sizes for turf and coralline algae, digitate and corymbose acroporids, and favids. Variograms for the coral reef system complement the CLSs estimated using Pascual and Levin's (1999) and Keeling *et al.*'s (1997) measures. In applied contexts, for example reserve design, we may be interested in defining a spatial scale which is weighted towards particular species that are important for economic or conservation reasons. In these cases, a 'toolbox' approach combining variogram analysis and CLS techniques would be useful for decision-making. CLSs provide an objective system-level measure, while variograms supply information about scales of spatial pattern of particular system components.

While nested ANOVA of hierarchically sampled spatial data has been widely and successfully applied for defining spatial scales of maximum variability in ecological analyses (Morrisey *et al.* 1992, Swadling *et al.* 1997, Dunstan and Johnson 1998, Graham and Edwards 2001), it is of limited use for identifying characteristic scales in the current study. For the model systems used here, nested ANOVA does little more than confirm that variability is highest at small spatial scales, while large scales are homogenous and hence have low variability. A particular disadvantage of nested ANOVA in the present context is its coarse sampling resolution, compared with window sampling and the spatial lagging approach of variograms. This coarse resolution is a likely reason for the failure of nested ANOVA to detect two scales of spatial variability in the 6- and 12-species systems.

Limitations and directions in estimating CLS

This thesis has developed valuable techniques for identifying CLSs that can potentially be applied to real ecological data sets. However, questions arise about the limitation and directions for CLS methods, in particular regarding (i) the robustness of CLS to subjective choices of embedding parameters, (ii) the assumptions underlying CLS approaches, and (iii) whether we expect to see meaningful CLSs for real ecological systems.

Robustness

As techniques for estimating CLSs become more sophisticated, there is a strong need to establish the robustness of these measures. Nichols and Nichols (2001) emphasise the importance of accurate attractor reconstruction in non-linear time series analysis, but note that the selection of parameters for attractor reconstruction is somewhat subjective. It is well recognized that the embedding delay τ and the embedding dimension d_E for attractor

reconstruction are not always defined clearly by mutual information and false nearest neighbour plots. Similarly, few algorithms have been developed for selecting the appropriate number of nearest neighbours, k, to determine predicted values on the reconstructed attractor. Sensitivity of CLSs to changes in τ, d_E and k has not been thoroughly assessed, even for the long time series approach. Analysis of the robustness of CLSs to all of these parameters is a necessary next stage in the development and assessment of techniques for estimating CLSs.

Another subjective step in the estimation of CLSs is identifying the asymptotic points for *prediction* r^2 and *error* X curves. Durrett and Levin (2000) developed a more precise definition to identify the scale at which *prediction* r^2 and *error* X curves attain the asymptote. However their definition, like any other, retains some element of subjectivity (i.e. in its definition of cutoff values for asymptotes). For practical purposes such as our present comparison of CLS estimation techniques, a range of scales containing the CLS is more meaningful than a point estimate. Indeed, for natural ecological systems that are variable in space and time, we would expect to measure slightly different CLSs on separate sampling occasions, and that these estimates would lie within some range of scales. More importantly, the CLS will not be the only piece of information in support of key applied decisions regarding spatial scales.

Assumptions

The techniques of Keeling *et al.* (1997) and Pascual and Levin (1999) estimate CLSs by comparing measures of variance in the dynamics at different window sizes. There are three important assumptions underlying this window sampling approach. The first assumption, that the maximum window size is larger than the CLS, is much easier to guarantee for models than for natural ecological systems. To ensure that the maximum sampling scale is large enough to include the CLS in a real system, we require some prior understanding of the general scales of dynamical processes.

A second assumption of the window sampling approach to estimating CLSs is that the largest window samples a single attractor. Non-linear time series analysis and prediction of data from more than one attractor will produce inaccurate CLS estimates. Sampling several attractors on one landscape is normally not a problem for models, but is a danger for natural systems. Selecting sampling scales for CLS analysis in natural systems will therefore involve a balance between sampling at a scale which is sufficiently large to capture CLS, but not so large as to

sample different domains of attraction. How to achieve this empirically, beyond using a 'trial-and-error' approach, is unclear.

The third assumption of Pascual and Levin's (1999) and Keeling *et al.*'s (1997) approaches to estimating CLSs is that ecological systems will exhibit a single CLS. Whether this assumption holds in Nature remains to be tested. It seems likely that systems such as zooplankton communities in the Southern Ocean, that have discrete patches at intermediate scales, but are strongly affected by large scale environmental processes (Hosie *et al.* 1997) could in fact be defined by a more than one CLS.

CLSs for real ecological systems

Further to this issue of whether we can expect a single CLS for ecological systems, is the question of whether CLSs are true *system* measures for ecosystems and communities. According to Takens' (1981) theory of attractor reconstruction, the dynamical information from a single species in a multi-species system should reflect, and indeed act as a substitute for, the unmeasured whole-system dynamic. But would we really expect the same CLS for pico-plankton and whales, or soil fauna and elephants in the same system?

Takens' (1981) attractor reconstruction theory, and hence the CLS estimation techniques of Pascual and Levin (1999) and Keeling *et al.* (1997) assumes full linkage between system components. In real ecological systems, however, component species may have weak dynamical associations. The coral reef model used in this study is an example of a system composed of species with different life histories, which in some cases interact very weakly with each other. The fact that CLS measures for this system were generally interpretable and consistent between species with different life histories is encouraging. More thorough investigation of the response of CLSs to differences in life histories and different degrees of dynamic linkage will be an important step in applying CLS techniques to real ecological systems. A related direction for future study is the development of multivariate CLS measures. A multivariate CLS would be a true system measure, and could be based on the multivariate non-linear time series analyses described by Muldoon *et al.* (1998) and Hegger and Schreiber (1992).

CONCLUSIONS

The short time series approach to estimating CLSs is a valuable alternative to the long time series techniques developed by Keeling *et al.* (1997) and Pascual and Levin (1999). Short time series analysis requires only three or four consecutive landscapes, and has the added advantage of being unaffected by non-stationarity over long time series. This approach to estimating CLSs could potentially be used to detect dynamic shifts in ecological systems, indicated by changes in the CLS. Preliminary investigations suggest that for the model systems in this study, the short time series technique is robust to the number of landscapes sampled and to the time step between landscapes. The second alternative to long time series methods – the sliding window approach – gives reasonable CLS estimates but some aspects of the results require further investigation, beyond the scope of this thesis.

While the problem of unrealistic data requirements for non-linear time series analysis has been described previously (Godfray and Blythe 1990, Keeling *et al.* 1997, Pascual and Levin 1999, Durrett and Levin 2000), this thesis is the first study to recognise other important limitations of the long time series approach to estimating CLS. These issues have not been identified before, because CLSs have only been estimated for model systems with limited numbers of species and simple spatio-temporal dynamics. Long time series results for the more complex systems in this study demonstrate substantial run-to-run variability in CLSs which is not clearly related to observed dynamics.

This thesis pioneers the transfer of CLS techniques from model systems to the real world. "Theory is most powerful when it provides new approaches that help resolve long-standing problems" (Kot *et al.* 1988). In truth, there is unlikely to be a single correct answer to the long-standing problem of defining characteristic scales in ecosystems. Nevertheless, in combination with other spatial approaches, the CLS will be a valuable tool for defining scales to observe, conserve and manage ecological systems.

LITERATURE CITED

Abarbanel, H. D. I. 1996. Analysis of Observed Chaotic Data. Springer-Verlag, New York, USA.

Bishop, M. J., A. J. Underwood, and P. Archambault. 2002. Sewage and environmental impacts on rocky shores: necessity of identifying relevant spatial scales. Marine Ecology Progress Series **236**: 121-128.

Castilla, J. C. 2000. Roles of experimental marine ecology in coastal management and conservation. Journal of Experimental Marine Biology and Ecology **250**: 3-21.

Dent, C. L., and N. B. Grimm. 1999. Spatial heterogeneity of stream water nutrient concentrations over successional time. Ecology **80**: 2283-2298.

De Roos, A. M., E. McCauley, and W. G. Wilson. 1991. Mobility versus density-limited predator-prey dynamics on different spatial scales. Proceedings of the Royal Society of London B **246**: 117-122.

Dunstan, P. K., and C. R. Johnson. 1998. Spatio-temporal variation in coral recruitment at different scales on Heron Reef, southern Great Barrier Reef. Coral Reefs **17(1)**: 71-81.

Durrett, R., and S. Levin. 2000. Lessons on pattern formation from the planet WATOR. Journal of Theoretical Ecology **205**: 201-214.

Ellner, S., and P. Turchin. 1995. Chaos in a noisy world: new methods and evidence from time-series analysis. The American Naturalist **145**: 343-375.

Fraser, A. M., and H. L. Swinney. 1986. Independent coordinates for strange attractors from mutual information. Physics Review A **33**: 1134-1140.

Garcia-Charton, J. A., and P. A. Perez-Rufaza. 1999. Ecological heterogeneity and the evaluation of the effects of marine reserves. Fisheries Research **42**: 1-20.

Godfray, H. C. J., and S. P. Blythe, S. P. 1990. Complex dynamics in multispecies communities. Philosophical Transactions of the Royal Society of London B **330**: 221-233.

Graham, M. H., and M. S. Edwards. 2001. Statistical significance versus fit: estimating the importance of individual factors in ecological analysis of variance. Oikos **93**: 505-513.

Greig-Smith, P. 1952. The use of random and contiguous quadrats in the study of the structure of plant communities. Annals of Botany, New Series **16**: 293-320.

Hegger, R., and T. Schreiber. 1992. A noise reduction method for multivariate time series. Physics Letters A **170**: 305-310.

Hosie, G. W., T. G. Cochran, T. Pauly, K. L. Beaumont, S. W. Wright, and J. A. Kitchener. 1997. The zooplankton community structure of Pyrdz Bay, January-February 1993. Proceedings of the NIPR Symposium on Polar Biology **10**: 90-133.

Johnson, C. R. 1997. Self-organising in spatial competition systems. Pages 245-263 *in* N. Klomp and I. Lunt, editors. Frontiers in Ecology. Elsevier, Oxford, UK.

Johnson, C. R., and P. K. Dunstan. 2002. Unpublished manuscript.

Johnson, C. R., and I. Seinen. 2002. Selection for restraint in competitive ability in spatial competition systems. Proceedings of the Royal Society of London B **269**: 655-663.

Kantz, H., and T. Schreiber. 1997. Nonlinear Time Series Analysis. Cambridge University Press, Cambridge, UK.

Kaplan, D., and L. Glass. 1995. Understanding Nonlinear Dynamics. Springer-Verlag, New York, USA.

Keeling, M. J., I. Mezic, R. J. Hendry, J. McGlade, and D. A. Rand. 1997. Characteristic length scales of spatial models in ecology via fluctuation analysis. Philosophical Transactions of the Royal Society of London B **352**: 1589-1601.

Kennel, M. B., R. Brown, and H. Abarbanel. 1992. Determining embedding dimension for phase-space reconstruction using a geometrical construction. Physics Review A **45**: 3403-3411.

Kershaw, K. A. 1957. The use of cover and frequency in the detection of pattern in plant communities. Ecology **38**: 291-299.

Kot, M., W. M. Schaffer, G. L. Truty, D. J. Graser, and L. F. Olsen. 1988. Changing criteria for imposing order. Ecological Modelling **43**: 75-110.

Lawrie, S. M., and C. D. McQuaid. 2001. Scales of mussel bed complexity: structure, associated biota and recruitment. Journal of Experimental Marine Biology and Ecology **257**: 135-161.

Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology **73**: 1943-1967.

Levin, S. A., and L. Buttel. 1986. Measures of Patchiness in Ecological Systems. Publication ERC-130, Ecosystem Research Center, Cornell University, Ithaca.

Morrisey, D. J., L. Howitt, A. J. Underwood, and J. S. Stark. 1992. Spatial variation in soft-sediment benthos. Marine Ecology Progress Series **81**: 197-204.

Muldoon, M. R., D. S. Broomhead, J. P. Huke, and R. Hegger. 1998. Delay embedding in the presence of dynamical noise. Dynamics and Stability of Systems **13**: 175-186.

Nichols, J. M., and J. D. Nichols. 2001. Attractor reconstruction for non-linear systems: a methodological note. Mathematical Biosciences **171**: 21-32.

O'Neill, R. V., R. H. Gardner, B. T. Milne, M. G. Turner, and B. Jackson. 1991. Heterogeneity and spatial hierarchies. Pages 85-96 *in* J. Kolasa and S. T. A. Pickett, editors. Ecological Heterogeneity. Springer-Verlag, New York, USA.

Palmer, M. W. 1988. Fractal geometry: a tool for describing spatial patterns of plant communities. Vegetatio **75**: 91-102.

Pascual, M., and S. A. Levin. 1999. From individuals to population densities: searching for the intermediate scale of nontrivial determinism. Ecology **80**: 2225-2236.

Plotnick, R. E., R. H. Gardner, W. W. Hargrove, K. Prestegaard, and M. Perlmutter. 1996. Lacunarity analysis: a general technique for the analysis of spatial patterns. Physical Review E **53**: 5461-5468.

Rand, D. A. 1994. Measuring and characterizing spatial patterns, dynamics and chaos in spatially extended systems and ecologies. Proceedings of the Royal Society of London A **348**: 497-514.

Rand, D. A., and H. B. Wilson. 1995. Using spatio-temporal chaos and intermediate-scale determinism to quantify spatially extended ecosystems. Proceedings of the Royal Society of London B **259**: 111-117.

Rossi, R. E., D. J. Mulla, A. G. Journel, and E. H. Franz. 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. Ecological Monographs **62**: 277-314.

Solé, R. V., and J. Bascompte. 1995. Measuring chaos from spatial information. Journal of Theoretical Biology **175**: 139-147.

Swadling, K. M., J. A. E. Gibson, D. A. Ritz, and P. D. Nichols. 1997. Horizontal patchiness in sympagic organisms of the Antarctic fast ice. Antarctic Science **9**: 399-406.

Takens, F. 1981. Detecting strange attractors in turbulence. Pages 366-381 *in* D. Rand and L. S. Young, editors. Dynamical Systems and Turbulence, Warwick, 1980. Lecture Notes in Mathematics 898. Springer-Verlag, New York, USA.

Tong, H. 1990. Non-linear Time Series Analysis. Oxford University Press, Oxford, UK.

Turchin, P. and A. D. Taylor. 1992. Complex dynamics in ecological time series. Ecology **73**: 289-305.

Underwood, A. J. 1981. Techniques of analysis of variance in experimental marine biology and ecology. Oceanography and Marine Biology Annual Review **19**: 513-605.

Underwood, A. J., and M. G. Chapman. 1998. Spatial analysis of intertidal assemblages on sheltered rocky shores. Australian Journal of Ecology **23**: 138-157.

Wiegert, R. G. 1962. The selection of an optimum quadrat size for sampling the standing crop of grasses and forbs. Ecology **43**: 125-129.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology **3**: 385-397.

Wilson, H. B., and M. J. Keeling. 2000. Spatial scales and low-dimensional deterministic dynamics. Pages 209-226 *in* U. Dieckmann, R. Law and J. A. J. Metz, editors. The Geometry of Ecological Interactions: Simplifying Spatial Complexity. Cambridge University Press, Cambridge, UK.

APPENDIX

The null case: no spatial pattern

The following proof shows that for a system with no spatial pattern (Fig A1) the expected values of *prediction* r^2 (Pascual and Levin 1999) and *error X* (Keeling *et al.* 1997) are constant. This theoretical result is confirmed by analysing time series of simulated landscapes (Fig A2).

Proof

Consider a time series of landscapes L_{ij}^t which are composed of independent, discrete valued pixels. The data series for a window of side length l is given by $N \sim Bin\left(l^2, \Pi\right)$ with $E(N) = l^2\Pi$ and $Var(N) = l^2\Pi(1-\Pi)$. The binomial distribution is used in preference to the normal distribution because the binomial gives discrete valued data and so provides a null case comparable with individual-based spatially explicit models containing species $X_1 - X_n$. The value Π can be thought of as the probability of observing a particular species X. The density of X in a window of side length l is $X_l^t = \frac{1}{l^2}\sum_{i=1}^{l}\sum_{j=1}^{l} L_{ij}^t = N^t/l^2$ and $E_t\left(X_l^t\right) = \Pi$.

By the Central Limit Theorem $Var\left(X_l^t\right) = \frac{1}{l^4} Var\left(N^t\right)$

$$= \frac{1}{l^4} l^2\Pi(1-\Pi)$$

$$= \frac{\Pi(1-\Pi)}{l^2} \qquad \text{(A1)}$$

Because the landscapes L_{ij}^t are independent, the X_l^t are also independent. So the k-nearest neighbours method averages k independent values of X_l^t to determine $\hat{X}_l^t$.

Therefore $E_t\left(\hat{X}_l^t\right) = E_t\left(X_l^t\right) = \Pi$ and $Var\left(\hat{X}_l^t\right) = Var\frac{1}{k}\sum_{i=1}^{k} X_l^{t_i}$

$$= \frac{1}{k^2} k \frac{\Pi(1-\Pi)}{l^2} \qquad \text{from (A1)}$$

$$= \frac{\Pi(1-\Pi)}{kl^2} \qquad \text{(A2)}$$

$\hat{X}_l^t$ and X_l^t are independent, so using (A1) and (A2)

$$Var\left(X_l^t - \hat{X}_l^t\right) = \frac{\Pi(1-\Pi)}{l^2} + \frac{\Pi(1-\Pi)}{kl^2} = \left(\frac{\Pi(1-\Pi)}{l^2}\right)\left(\frac{k+1}{k}\right) \qquad \text{(A3)}$$

Since $E_t\left(X_l^t - \hat{X}_l^t\right) = 0$ then $Var\left(X_l^t - \hat{X}_l^t\right) = E_t\left[\left(X_l^t - \hat{X}_l^t\right) - E_t\left(X_l^t - \hat{X}_l^t\right)^2\right]$

$$= E_t\left[\left(X_l^t - \hat{X}_l^t\right)^2\right] - E_t\left(X_l^t - \hat{X}_l^t\right)^2$$

$$= E_t\left[\left(X_l^t - \hat{X}_l^t\right)^2\right] \qquad \text{(A4)}$$

Together (A3) and (A4) give $E_t\left[\left(X_l^t - \hat{X}_l^t\right)^2\right] = \left(\frac{\Pi(1-\Pi)}{l^2}\right)\left(\frac{k+1}{k}\right)$ which is used to predict values of the CLS statistics:

- Keeling *et al.* (1997)'s *error* $X = l\sqrt{E_t\left[\left(X_l^t - \hat{X}_l^t\right)^2\right]}$

$$= l\frac{\sqrt{\Pi(1-\Pi)}}{l}\sqrt{\frac{k+1}{k}}$$

$$= \sqrt{\Pi(1-\Pi)\left(\frac{k+1}{k}\right)}$$

- Pascual and Levin's (1999) *prediction* $r^2 = 1 - \frac{E_t\left[\left(X_l^t - \hat{X}_l^t\right)^2\right]}{Var\left(X_l^t\right)}$

$$= 1 - \frac{\left(\frac{\Pi(1-\Pi)}{l^2}\right)\left(\frac{k+1}{k}\right)}{\left(\frac{\Pi(1-\Pi)}{l^2}\right)} = -\frac{1}{k}$$

Expected values of *prediction* r^2 and *error* X for the null case are validated here using a series of landscapes with $\Pi = 0.3$ and $k = 10$ (Fig A2). Expected values are

prediction $r^2 = -\frac{1}{k} = -0.1$ and *error* $X = \sqrt{\Pi(1-\Pi)\left(\frac{k+1}{k}\right)} = \sqrt{0.21 \times 1.1} = 0.48$.

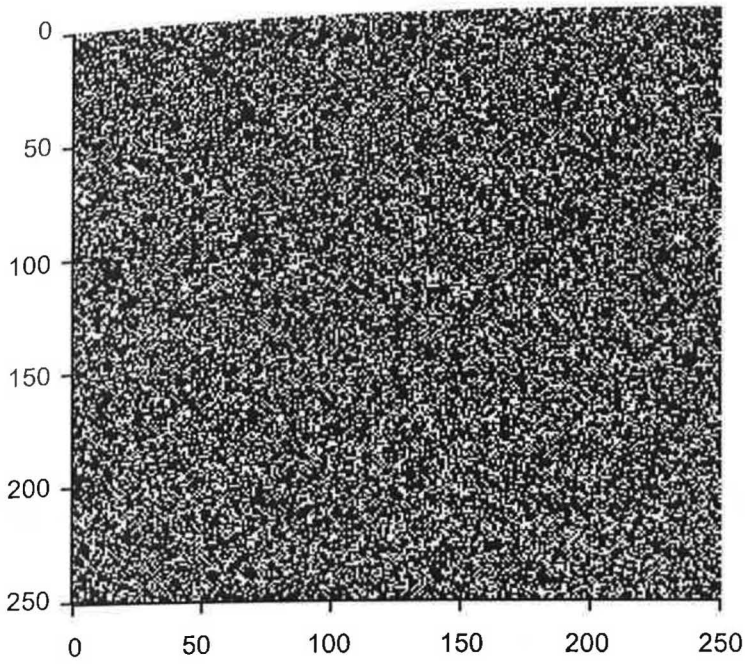


Figure A1 250 × 250 landscape of independent, discrete pixels. White pixels occur with frequency 0.3.Time series of simulated landscapes like this one were used to generate the results in **Figure A2**.

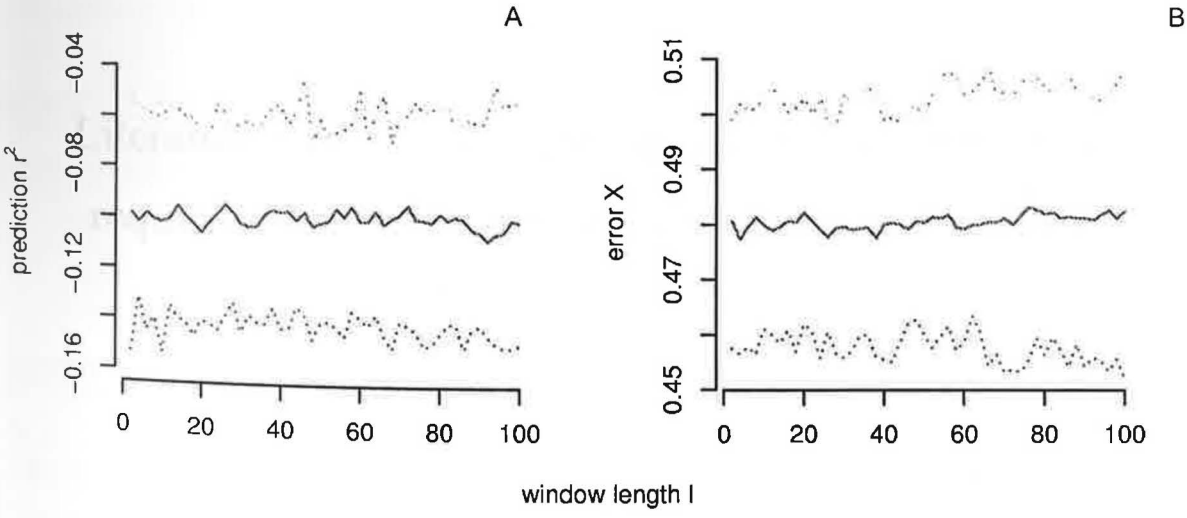


Figure A2 Results for long time series analysis of 1000 simulated frames of independent, discrete valued pixels. **A** *Prediction* r^2, **B** *error X*. $\tau = 1$, $d_E = 5$, $k = 10$. Landscape size is 100 × 100 pixels. Solid lines indicate average curves for 100 replications and dotted lines indicate 95% confidence intervals. The expected values for the null case of independent discrete pixels are (*prediction* $r^2 = 0.10$ and *error* $X = 0.48$) are confirmed in this empirical analysis.

Techniques for estimating characteristic length scales and their potential for application to natural systems

Jessica Trebilco B.Sc

Literature Review submitted in partial fulfilment of the requirements for a Bachelor of Science with Honours

School of Zoology
University of Tasmania
2002

TABLE OF CONTENTS

INTRODUCTION

Ecological processes take place on a range of spatial scales. To fully understand these processes it is necessary to view them on a suitable scale. The question of how to determine appropriate scales for studying ecosystems has been investigated by ecologists since the 1950s. Greig-Smith (1952) and Kershaw (1957) attempted to describe the scale of spatial patterns in vegetation. Improved analyses have been developed by Usher (1969), Errington (1973), Hill (1973), Usher (1975), Ripley (1978) and Ludwig (1979). Recently, the explicit inclusion of space in computer models of ecosystems has again emphasized the importance of spatial patterns in the dynamics of ecosystems (Durrett and Levin, 1994a, b; Johnson, 1997; Durrett and Levin, 1998; Durrett and Levin, 2000).

An important question is whether a characteristic spatial scale, or "characteristic length scale" (CLS) can be defined for patterns in ecosystems. A CLS should be inherent to a system, and would provide an appropriate scale at which to study the dynamics of the system (Wiens, 1989; Levin, 1992). Various measures have been developed to estimate the CLS of a system, based on variance within the system in space or in time (De Roos *et al.*, 1991; Rand, 1994; Rand and Wilson, 1995; Keeling *et al.*, 1997; Zöller *et al.*, 1998; Pascual and Levin, 1999; Wilson and Keeling, 2000; Durrett and Levin, 2000). These techniques define an intermediate scale at which to observe dynamics, where meaningful signal is maximized and noise is minimized.

The estimation of CLSs in natural systems could be very useful for determining suitable reserve sizes and management units, as well as scales for monitoring particular systems or components of systems. Specific applications of CLSs include epidemiology (Levin *et al.*, 1997), ecotoxicology (Johnson, A. R. 2002), and the study of networks including foodwebs and neural networks (Levin *et al.*, 1997). Rand and Wilson (1995) suggest using CLS methodology to detect shifts in ecosystem dynamics.

While techniques for characterizing pattern in vegetation have been applied to field data, modern approaches to defining CLSs have predominantly used data from models. Johnson (2002) outlines the following requirements for CLSs to be applied to natural systems:

1) Methods must be appropriate to the complicated spatial and temporal dynamics of natural systems.
2) It must be possible to collect sufficient data from real systems to estimate CLSs.
3) CLS measures must be robust. Specifically, different variables from the same system should give similar estimates of the CLS, and space-time variation in CLSs should be small (unless there is significant change within a system).

This review traces the development of methods to identify scales of pattern in ecosystems and to determine ecosystem CLSs. The potential for application of CLS estimation techniques to natural systems is addressed in terms of Johnson's (2002) three requirements.

TECHNIQUES FOR ESTIMATING CLSs

The general approach for estimating the CLS of a system is to view the system through "windows" of different sizes. Schneider (1994) distinguishes between the operations of zooming and lagging. Zooming is the process of combining small windows to form larger windows, while lagging examines at windows at successively greater separations. Methods for estimating CLSs tend to use zooming, but some measures adopt a lagging approach to describe the scale of spatial patterns (for example, spectral analysis, correlograms and variograms).

CLSs are determined by the scaling of the variance of some system parameter. In natural systems there is often a decrease in variance with increasing window size. Small windows will show large fluctuations either between windows at one point in time, or in the same window at successive points in time. In large windows, fluctuations tend to be averaged out. The CLS of a system is some intermediate window size, where the fluctuations over space or time are meaningful (deterministic).

For the following discussion it should be noted that the term ***length*** in characteristic length scale distinguishes a spatial scale from a time scale. Length may refer to a linear distance or to an area,

depending on the method. Also, the description of techniques for characterizing patch size is not comprehensive, but provides an important background for understanding modern methods for estimating CLSs. The evolution of techniques has largely been driven by statistical improvements and attempts to accommodate the complex dynamics of natural systems.

Block size analysis of variance

Block size analysis of variance was developed to detect and quantify pattern in plant communities sampled with quadrats. The method compares variances of quadrats grouped into larger and larger windows (blocks). Greig-Smith (1952) used this approach with nested quadrats. He combined adjacent pairs of quadrats to give two-quadrat blocks, then adjacent two-quadrat blocks into four-quadrat blocks, and so on.

Greig-Smith (1952) used nested analysis of variance of block sizes, and plotted mean square against block size. In such a plot, different scales of pattern in the data appear as peaks or troughs (Goodall, 1974). Kershaw (1957) extended Greig-Smith's (1952) method to contiguous quadrats arranged in a row rather than in blocks. Peaks on the mean square versus block size plot indicate the linear dimensions of patches rather than their area.

Turner *et al.* (1991) summarize criticisms of blocking methods:

1. The methods of Greig-Smith (1952) and Kershaw (1957) are sensitive to the starting position of the analysis. Estimates of the size of patches may change by a factor of two with different starting positions (Ripley, 1978). Usher (1969) suggested using various starting positions and selecting the maximum block-size estimate as the 'true' position of a peak. This is unsatisfactory because it introduces an element of arbitrariness even greater than that which it eliminates (Errington, 1973). Another approach is to average a number of blocked-quadrat analyses with different starting positions (obtained by stepping progressively along the transect) (Usher, 1975).
2. The initial choice of quadrat size is arbitrary (Ripley, 1978), and once it is chosen a set of quadrat spacings at block sizes 1, 2, 4, 8, 16, 32, 64, etc. are imposed (Ludwig, 1979). This means that the system is only sampled at a limited number of block sizes, and patterns at scales between these block sizes are not detected. Hill (1973) proposed a

"two-term local variance" method which involves calculating variances over all block sizes up to one-half the total number of quadrats. This method eliminates the problem of power-of-two sampling.

3. There is no statistical technique to test the significance of the peaks found in the mean square by block size plot. Greig-Smith (1964) suggests that subjective assessment of peaks may not be too great a problem if a series of analyses are performed. If a peak recurs in the same position or shows regular drift in a series of related systems there can be little doubt of its validity.

Ludwig (1979) concludes that Hill's (1973) method provides the most accurate evaluation of the scales and intensity of patterns in vegetation. This method also reduces the problems associated with starting position. However, it requires more sampling and computational effort than other blocking approaches, and when two scales of pattern exist, Hill's (1973) technique emphasizes the pattern at the larger scale.

Carlile *et al.* (1989) describe a technique which combines blocking with spatial autocorrelation analysis (described below). Carlile *et al.* (1989) calculated and compared the correlation coefficient for different transect lengths. The statistical rigor of their method has not been evaluated (Turner *et al.*, 1997).

Correlograms and variograms

Correlograms summarize information obtained through autocorrelation analysis (Sokal and Oden, 1978a, b). Autocorrelation tests whether the observed value of a variable in one window is significantly dependent on observed values of the variable in other windows. If all possible pairs of windows are compared, the positions of strong similarity (and dissimilarity) will be found (Cliff *et al.*, 1975). This method is a spatial lagging approach, as opposed to the zooming used in block size analysis of variance. The distance between any two windows is referred to as a lag. Lag-one analysis compares adjacent windows. For a lag-two analysis, the cross-comparison is made at a displacement length of two sample units. Comparisons are usually calculated for lags from zero to one-fourth the total number of samples (Davis, 1986).

Dependency between windows is measured as autocorrelation, which is plotted against lag length in a correlogram. Correlograms summarize patterns of geographic variability, with peaks above zero suggesting the scale of patches (Sokal and Oden, 1978a, b). The homogeneity and arrangement of patches are also reflected in correlograms.

Variograms are produced in a similar way to correlograms. A type of variogram called a semivariogram is particularly useful for ecological analyses (Palmer, 1988; Rossi *et al.*, 1992; Dent and Grimm, 1999). Semivariance is a measure of the degree of dependence between windows. A semivariogram is a plot of semivariance at different distances or spatial lags. Flat regions called sills on semivariogram plots suggest the scale of patches (Palmer, 1988). Note that the scale suggested by correlograms and semivariograms is a length, rather than the area measure from block size analysis of variance.

Rossi *et al.* (1992) present a critique of variogram and correlogram analyses. Variograms can provide an incomplete or misleading summary of spatial pattern when local means and variances change. While correlograms accommodate changing local variances and means, this form of analysis is less useful for data with outliers. Rossi *et al.* (1992) suggest that a combination of techniques should be used to obtain more accurate information about the scale of patterns in ecosystems.

Spectral analysis

Spectral analysis is another lagging approach for determining patch size in vegetation. This technique identifies pattern in a data sequence by expressing the observations as a combination of wave functions – usually sine and cosine waves. Block-size analyses can be considered as spectral analysis using square waves (Ripley, 1978). Platt and Denman (1975) describe spectral analysis of time series data, but their approach does not focus on characterizing the scale of spatial patterns.

Spectral analysis is a variance approach because the sum of the variation in all the waves used to represent the data series must be equal to the total variation in the data (Turner *et al.*, 1991). The

product of spectral analysis is a periodogram: a variance plot used to determine the frequency, or scale, of patterns.

According to Turner *et al.* (1991), spectral analysis can handle a complexity of information that is insurmountable by other methods. Because it is a sine and cosine transformation, it is not subject to error due to the starting position of sampling (Ripley, 1978). Usher (1975) points out that spectral analysis is particularly suited to analyzing small scale patterns, but it is very insensitive to patterns on a larger scale. Spectral analysis assumes that the system is linear (Hill, 1973), and that the data are statistically stationary (there are no spatial trends) (Turner *et al.*, 1991). This is true of all the vegetation analysis methods described so far. However, nonlinearity and nonstationarity are often present in natural systems.

Another issue with the measures of pattern and patch size described above is that while they do characterize ecosystems, they do not necessarily indicate appropriate scales for observation. Natural systems often have multiple scales of pattern, and it is difficult to choose the most appropriate of these scales. None of the measures described include a temporal aspect in variance estimates. Dynamics through time are often crucial for understanding natural systems, for example predator prey cycles, or temporal succession in vegetation. Block size analysis of variance, autocorrelation, semivariance and spectral analysis are useful for characterizing pattern, but may be too simplistic for estimating CLSs of complex systems.

Variance staircase and temporal CV

Variance changes with the scale of sampling. In general, sample variance s^2 is inversely proportional to window area. If the sampled population is randomly distributed in space so that each new sample is independent of previous samples, then plotting ln (s^2) against ln (window size) will give a straight line with slope –1. Smith (1938) pointed out that if significant spatial correlation exists (samples are not independent) then the slope of this variance decay plot will lie between –1 and 0.

Weigert (1962) used variance decay plots for nested quadrats to determine the appropriate quadrat size to sample vegetation. Levin and Buttel (1986) suggested that changes in the slope of

variance decay plots can be used to determine patch size. The scale at which variance asymptotes to a slope of –1 is called the correlation length (Ma, 1976). This scale can be thought of as a CLS for ecosystems. O'Neill *et al.* (1991) used a variance decay plot, which they dubbed the "variance staircase", to analyse remotely sensed land use data. They found multiple scales of variation, represented as plateaus in the variance plot, which were interspersed with linear regions of slope –1 (Fig 1).

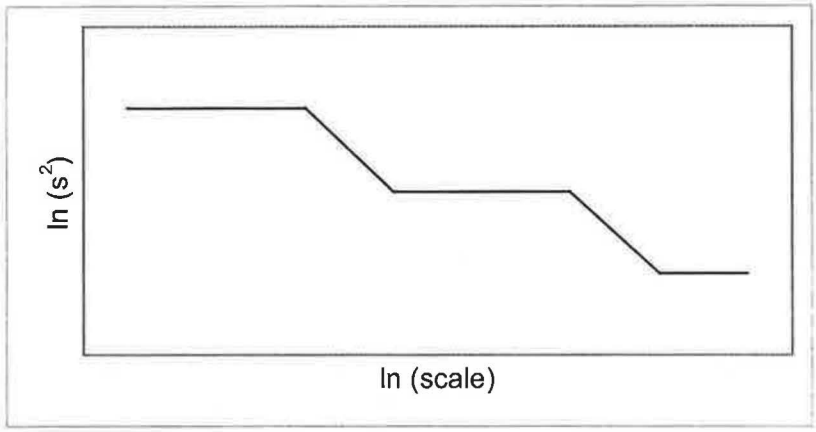


Figure 1 Generalised shape of the "variance staircase". The plateau regions correspond spatial scales at which processes act to structure the landscape.

Temporal CV looks at population dynamics through time in windows of increasing size (it is a zooming approach). Crowley (1977) suggested that there is a relationship between the temporal coefficient of variance (CV = standard deviation/mean) and window size for animal populations. Within small windows populations should fluctuate synchronously, but small windows that are far apart will be subject to different random influences, and so will fluctuate asynchronously. The variance of small windows over time should be greater than the variance of larger windows. This is because population fluctuations within large windows tend to cancel out, leading to decreased variance.

The expected result of plotting temporal CV against window size is a linear decrease with low slope at small scales, followed by a steeper, but still linear decrease above a certain threshold scale (De Roos *et al.*, 1991). This threshold can be regarded as the CLS of a system. De Roos *et al.* (1991) used temporal CV plots to analyse a spatially explicit predator prey model. They

defined the CLS as the point of divergence of temporal CV plots (of prey density) for homogeneous predator movement and for diffusive predator movement (Fig 2).

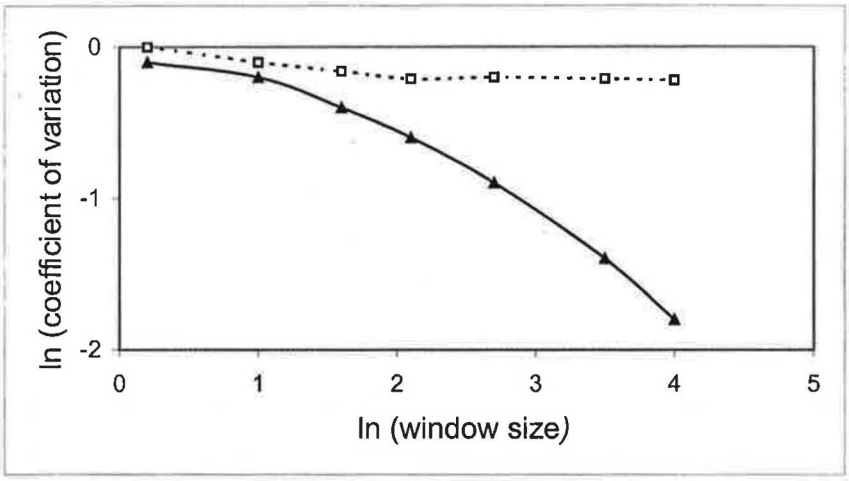


Figure 2 Coefficient of variation in prey density over simulated time series, at different spatial scales. The CLS is the scale where homogenous predator movement (open squares), diffusive predator movement (closed triangles) diverge. After De Roos *et al.* (1991)

While both the variance staircase and temporal CV methods use variance plots to determine a CLS, the CLS estimate for the former refers to a linear distance, while that for the latter is an area measure. Furthermore, the variance staircase method uses measures of variance in space, while temporal CV uses variance over time. Given these underlying differences, Tyre *et al.* (1997) compared the CLS estimates from the two techniques for model output and for a real biological data set.

Temporal CV is related to population dynamics over time, so a CLS measured this way should reflect the strength of processes like dispersal and disturbance that influence dynamics. However, Tyre *et al.* (1997) found that for a model system, neither the variance staircase nor the temporal CV method detected differences between global and local disturbance scenarios. The results of applying the two CLS measures to real data were also ambiguous. This may be because both methods assume stationarity and linearity in the data. Tyre *et al.* (1997) point out that the assumption of stationarity may be less critical for the temporal CV analysis, because the

coefficient of variance is a relative measure. The average population density might vary tremendously in space without affecting the temporal CV.

The computation and interpretation of variance decay plots and temporal CV are fairly arbitrary. As with blocking methods, the starting point of the analysis can affect the results (Tyre *et al.*, 1997). Determining where slopes changes on variance decay plots is also a matter of judgment. O'Neill *et al.* (1991) used an iterative procedure of calculating a regression slope, predicting the next point, and then either adding it in if correctly predicted, or using it as the starting point for a new slope. Tyre *et al.* (1997) claim that this procedure has dubious statistical validity at best.

The approaches outlined in this section can be applied to systems where variance decreases with increasing scale of observation. Schneider (1994) questions this relationship for natural systems. Schneider (1994) suggests that variability may increase with sampling scale depending on the life history characteristics of the organisms in the system, and their responses to environmental factors (for example, climatic factors may be more variable on larger scales). One such case may be aquatic systems. According to Powell (1989), the variance-sampling scale relationship in aquatic systems is opposite to that in terrestrial systems. While variance has been found to decrease with increasing sampling scale for some plant communities (Moloney *et al.*, 1992) and for model output (Levin and Buttel, 1987), there has been no extensive study of the variance-scale relationship in natural systems.

Fluctuation analysis

In ecological systems stochasticity (random fluctuation) prevails at small scales, while at large scales, small fluctuations around a steady state result from averaging local dynamics that are out of phase. According to Rand and Wilson (1995) there is an intermediate scale where a system oscillates in a predictable (deterministic) way. Rand and Wilson (1995) propose this scale as the optimal scale for observing the dynamics of a system (the CLS).

The CLS extracted by Rand and Wilson (1995) is the scale at which parts of the landscape begin to act independently. Like previous methods, their approach examines scaling of the variance in a window of dimensions L × L. If the density of one species (S_L) is determined for L × L windows

through time, then the variance var(S_L) can be calculated for each window size. Rand and Wilson (1995) plotted var(S_L)/L^2 against L, and defined the CLS to be the point where the curve asymptotes to a constant value (Fig 3). Above this scale, there is no proportional increase in variance, so the CLS represents the scale at which windows become statistically independent.

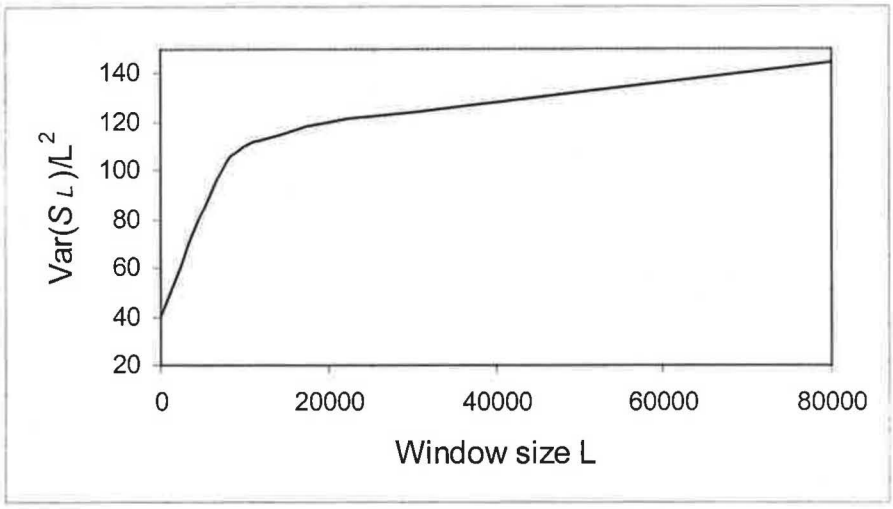


Figure 3 Rand and Wilson's (1995) measure of relative variance plotted against window size. The CLS is the scale where the graph becomes linear.

Rand and Wilson (1995) tested whether the dynamics at the CLS selected for their model system were deterministic. They used non-linear time series analysis methods from statistical physics as an *a posteriori* test for determinism. Keeling *et al.* (1997) incorporated the same non-linear time series analysis methods in an improved approach for estimating CLSs. The CLS of Keeling *et al.* (1997) is more suitable for systems with oscillatory dynamics which differ from random fluctuations around a global average.

Keeling *et al.* (1997) use a variance approach called fluctuation analysis. To calculate variance, the average value for the system must be known. Rand and Wilson (1995) used the global average of their model system to calculate variance. Keeling *et al.* (1997) instead consider deviations from some underlying deterministic behaviour, varying in time. This underlying behaviour is modeled using prediction algorithms from nonlinear time series analysis (Casdagli,

1989). Keeling *et al.* (1997) use their variance plot (or fluctuation diagram) to determine the CLS, and to identify aggregation at various scales.

The approach of Keeling *et al.* (1997) is more appropriate to the complex nature of real systems than Rand and Wilson's (1995) CLS measure. However, Durrett and Levin (2000) note that a problem with both methods is the subjectivity in defining the scale at which the fluctuation diagram asymptotes. Durrett and Levin (2000) provide a more precise definition for this scale. Keeling *et al.* (1997) point out that to rigorously justify their method (and that of Rand and Wilson, 1995) it is necessary to have exponential decay of correlations between observations with increasing separation. Unfortunately, correlations can be difficult to analyse (Keeling, *et al.*, 1997).

Determinism tests

The CLS measure developed by Pascual and Levin (1999) complements Keeling *et al.*'s (1997) fluctuation analysis method. Pascual and Levin's (1999) approach compares the degree of determinism in population dynamics across different window sizes, using a determinism test from nonlinear time series analysis. At a given window size, the degree of determinism is evaluated from the prediction accuracy of a predication algorithm (Kaplan and Glass, 1995) established from the data. Prediction accuracy is determined by comparing the error in predictions from the algorithm with the variance of the time series.

The first step in Pascual and Levin's (1999) method is to develop a prediction algorithm. This involves the technique of attractor reconstruction (Takens, 1981). Attractor reconstruction uses time series data from a single variable $x(t)$ to reconstruct the general shape of a system's dynamics (the attractor) in n-dimensional phase space. The reconstructed attractor is topologically equivalent to the real attractor which could be obtained by measuring all the variables in the system. The procedure for reconstruction is called embedding, and uses past values of $x(t)$ as surrogates for the unobserved variables in the system.

Time-delayed coordinates for the reconstructed attractor are

$$x(t), x(t - \tau), x(t - 2\tau), \ldots, x(t - (d_E - 1)\tau)$$

Here, τ is the selected time delay, or lag and d_E is known as the embedding dimension. The embedding dimension can be thought of as how far in the past it is necessary to look for an explanation of current changes. Appropriate values of τ and d_E can be estimated from the data itself (Nichols and Nichols, 2001).

Pascual and Levin (1999) select τ as the value for which the autocorrelation function first crosses zero and d_E is chosen using the concept of false nearest neighbours (FNN). If d_E is too small, then points that are far apart in phase space can appear close because of a projection effect; they are false neighbours. As soon as d_E is high enough, the reconstructed attractor is completely unfolded so that neighbours in phase space truly result from the dynamics returning to similar states. To illustrate, consider a figure 8 in 2-dimensional space. Points near the crossing of this symbol are near neighbours. However, in 3-dimensions the figure 8 may be unfolded, so that points at the cross-over are longer be neighbours.

The concept of decreasing false nearest neighbours with increasing dimensions for the attractor of a model system is presented in Figure 5. Pascual and Levin (1999) use an algorithm to select d_E based on estimation of the percentage of false nearest neighbours for increasing trial values of d_E.

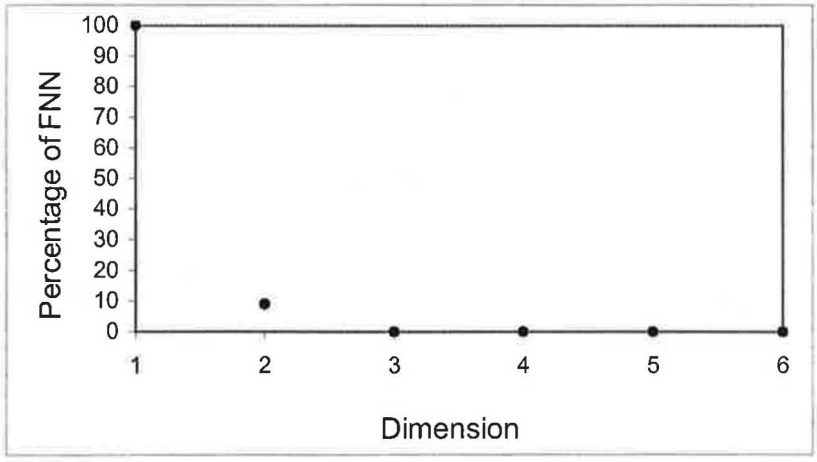


Figure 4 The percentage of false nearest neighbours (FNN) with increasing embedding dimensions for a weather system model (the Lorenz model). After Abarbanel (1996).

The second step in Pascual and Levin's (1999) method for estimating CLSs involves assessing the prediction accuracy of the prediction algorithm. A nearest neighbours approach is used to predict where a point $z(t)$ in the original time series will be h units of time later. The positions of the k nearest neighbours of $Z(t)$ ($z(t)$'s equivalent point in reconstructed phase space) at time $t + h$ are averaged to give a prediction for the position of $Z(t + h)$. This is compared with the actual value of $z(t + h)$ in the original time series with a statistic called prediction r^2. This statistic is a measure of determinism, since high predictability (and hence high r^2) implies determinism.

A plot of prediction r^2 against window size is used to indicate the scale of maximum determinism – the CLS of the system (Fig 5). Once a CLS estimate has been obtained, Pascual and Levin (1999) perform a further analysis of the system dynamics at this scale. By calculating the correlation dimension at the CLS they confirm that the system has a finite dimensional attractor, which is evidence for deterministic dynamics.

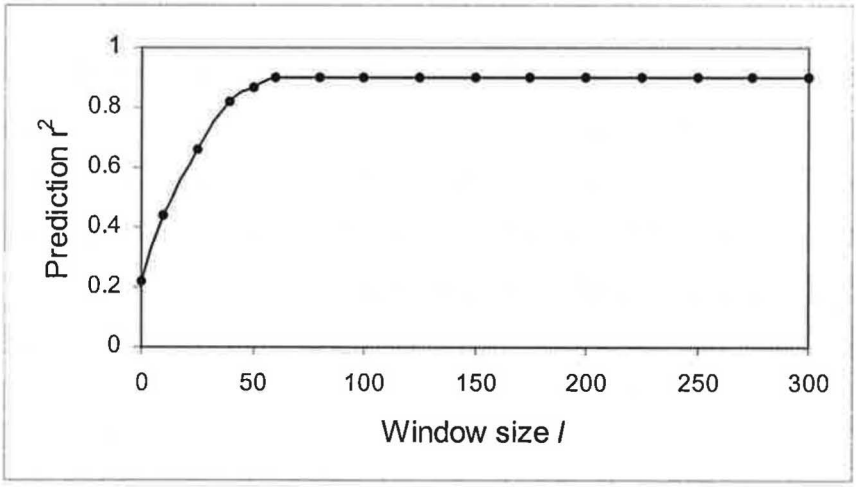


Figure 5 Prediction r^2 as a function of window size for the model system used by Pascual and Levin (1999). The CLS is the scale where prediction r^2 asymptotes.

Nichols and Nichols (2001) emphasize that accurate attractor reconstruction is critically important for the development of a useful prediction algorithm and hence to obtaining a good estimate of prediction error. Accurate reconstruction depends on the choice of time lags and embedding dimension. Nichols and Nichols (2001) show that the use of autocorrelation to

determine an appropriate lag may be inappropriate since autocorrelation is a linear based technique. Instead, they advocate choosing τ as the first minimum of the mutual information function. Mutual information is the information gained about the value of $s(t + \tau)$, given $s(t)$ (Abarbanel, 1996).

Time delays and embedding dimensions are chosen subjectively. If mutual information plots are used, then the investigator must determine where the first minimum on the plot occurs (this is likely to change with window size). Where the autocorrelation function is used, the choice of the threshold value defining τ (0.00 or 0.05) is arbitrary. In terms of embedding dimensions, the percentage of false nearest neighbours will never drop to zero for real systems with noise. Thus, it is necessary to choose what percentage of false nearest neighbours is acceptable. Pascual and Levin (1999) give no indication of whether their chosen values of τ and d_E vary between window sizes. This would seem appropriate since determinism and therefore the dimension of the attractor will vary with the scale of observation.

The selection of the k nearest neighbours and the algorithm for averaging their position is important for evaluating prediction accuracy of the prediction algorithm. The choice of k is subjective, and there are alternative averaging algorithms to the one selected by Pascual and Levin (1999) which may be more suitable (Nichols and Nichols, 2001). A potential problem with Pascual and Levin's (1999) method arises if the attractor for the system is shifting in phase space. A shifting attractor cannot necessarily be detected from the data, and may affect prediction algorithms.

Zöller *et al.* (1998) describe a different kind of determinism test which they use to estimate CLSs of non-biological models and of earthquake data. They adopt an approach developed by Pei and Moss (1996) using a test for unstable periodic orbits. For a certain point x_0, Zöller *et al.* (1998) consider a set of time series calculated by averaging the data in a circular window around x_0. The time series for different window sizes are compared with respect to the occurrence of nonlinear determinism in the data. This idea is similar to Pascual and Levin's (1999) technique, except for the use of circular windows instead of L × L squares.

The main difference between the approaches of Pascual and Levin (1999) and Zöller *et al.* (1998) is that the latter approach uses the occurrence of unstable periodic orbits as a measure of nonlinear determinism. Zöller *et al.*'s (1998) CLS is the scale at which the occurrence of unstable periodic orbits is significantly greater than at other scales. Statistical significance is derived from a comparison of the original data with appropriate surrogate data. Zöller *et al.* (1998) obtain surrogate data by phase randomization and amplitude adjustment of the original data, but suggest other methods might also be appropriate.

The validity of Zöller *et al.*'s (1998) method for estimating CLSs in biological systems has not been formally assessed. One apparent advantage of this method is that there are fewer subjective choices (of time lags, embedding dimensions or k nearest neighbours). Zöller *et al.*'s (1998) approach uses round windows rather than square windows. This shape could be more appropriate for sampling in ecological systems where colonies or clumps are often closer to circular than to rectangular. In contrast to other methods, Zöller *et al.* (1998) do not use a variance approach to determine the CLS, but instead look directly at changes in determinism with window size.

Comparison of techniques

The approaches of Keeling *et al.* (1997) and of Pascual and Levin (1999) are most desirable among the techniques for estimating CLSs which have been outlined. Fluctuation analysis and determinism tests are area measures which include a temporal aspect and accommodate oscillatory dynamics. The two measures applied to the same data set give different answers (Pascual and Levin, 1999; Durrett and Levin, 2000), raising the question of which provides the best estimate of the CLS of a system.

Pascual and Levin (1999) point out that maximum determinism can occur at a smaller scale than that required for the onset of independence. They suggest that their determinism test is complementary to fluctuation analysis, with the two CLS measures providing a range of scales for sampling. Durrett and Levin (2000) emphasize that no formula for the CLS of a system gives the "right answer".

Fluctuation analysis and determinism tests are clearly more appropriate to the complex dynamics of biological systems. However, these CLS measures correspond fairly closely to the correlation length (the scale where variance asymptotes to a slope of –1, Ma, 1976) of *spatial* patterns, calculated for the same model systems. It would be useful to investigate whether simple spatial measures and complex dynamical CLSs (from fluctuation analysis and determinism tests) generally correspond. This could be examined in model systems by comparing distributions of correlation lengths with CLSs from multiple model runs. No difference between the distributions would advocate using the simpler measures requiring less sampling and computational effort. Correspondence of spatial measures with the CLSs of Pascual and Levin (1999) or Keeling *et al.* (1997) seems less probable in real systems, where the dynamics are likely to be nonlinear and nonstationary.

The role of noise

A key issue throughout this discussion has been whether CLS measures are appropriate to the complex spatial and temporal dynamics of natural systems. While the CLS estimation techniques of Keeling *et al.* (1997) and Pascual and Levin (1999) take into account nonstationarity and complex non-linear dynamics (both of which occur in natural systems) these methods assume that, at some spatial scale, the determinism in ecosystem dynamics reaches a maximum. Questions have recently been raised regarding the role of noise in ecological systems, and how this affects assumptions about determinism in nonlinear time series analysis (Ellner and Turchin, 1995; Pascual *et al.*, 2001).

Noise arises from unpredictable, density independent perturbations, and occurs in any natural system (Ellner and Turchin, 1995). Pascual *et al.* (2001) found that noise produced by individual variation plays an essential role in determining properties of the dynamics of a system, such as their dominant period, power spectra and sensitivity to initial conditions. Pascual *et al.* (2001) argue that this finding casts some doubt on the viability of a fully deterministic approximation for estimating CLSs.

The intermediate scale defined as the CLS is nonetheless important. Sampling of real systems at this scale can provide reasonable parameters for modeling densities at larger scales, when

sampling efforts at those scales are difficult or prohibitive (Pascual *et al.*, 2001). Thus, even if noise is more important than previously thought in ecosystems, it is useful to collect data and to observe systems at their CLS. A critical question is whether sufficient data can be obtained from natural systems to determine their CLSs.

CAN DATA FROM REAL SYSTEMS BE USED TO ESTIAMTE CLSS?

The major obstacle to measuring CLSs of natural systems using the methods of Pascual and Levin (1999) and Keeling *et al.* (1997) is the quantity of data needed. Fluctuation analyses and determinism tests have been applied exclusively to model output; thousands of generations sampled at landscapes of at least ten thousand pixels. Such large quantities of data can rarely, if ever, be collected for real ecosystems. There is a need to refine these methods for estimating CLSs so that their data requirements are reduced and they can be applied to real systems.

Data requirements

The majority of techniques for quantifying pattern and extracting CLSs require large and complete data sets in space and/or time. According to Turner *et al.* (1991), these restrictions may limit blocking procedures to detecting scales of patterns on fairly small landscapes, unless remotely sensed data is available. Spectral analysis can be used to detect complex patterns in ecosystems. However, it requires equally spaced data without missing values (Turner *et al.*, 1991), and where time series data are involved, long time series are needed. While equally spaced data may be obtained from unequal spacings by interpolation (Platt and Denman, 1975), sampling must still be intensive to achieve sufficient quantities of data.

Jumars *et al.* (1977) point out that although autocorrelation coefficients do not convey the amount of information obtained from spectral analysis, they require a much smaller number of samples and a less constrained sampling pattern. The calculation of autocorrelation coefficients can be used as a preliminary test to determine whether the additional effort required to perform spectral analysis seems worthwhile (Jumars *et al.*, 1977).

The variance staircase and temporal CV approaches are also data intensive. To calculate the temporal coefficient of variance, data must be available from multiple points in time. Time series data are also required for fluctuation analysis and for determinism tests. It is very rare to have detailed time series of spatially resolved data from natural systems. The data requirements for Pascual and Levin's (1999) *a posteriori* analysis (to estimate the dimensionality of the attractor) are even greater than for the determinism test. The quantity of data needed to estimate attractor dimensionality is not within the realm of most ecological time series.

Application of techniques to real data versus artificial data

Vegetation analysis methods were developed primarily for the analysis of real data. Robustness tests were performed using artificial data sets. This approach was used, for example, by Greig-Smith (1952), Sokal and Oden (1978a, b) and Ripley (1978). Tyre *et al.* (1997) applied variance staircase and temporal CV analyses to a single-species, spatially explicit population model and to real data from a lizard population. Using the model data, Tyre *et al.* (1997) assessed how the CLS estimates responded to changes in model parameters, such as rates of dispersal. Estimation of CLSs for real data was less successful than for model data, most likely because both methods assume stationarity of variances. The comparative approach adopted by Tyre *et al.* (1997) would be very useful if repeated for fluctuation analysis and determinism tests.

Fluctuation analysis and determinism tests have only been applied to model data. Common model systems used for analysis are predator-prey systems (De Roos *et al.*, 1991; Pascual and Levin, 1999) and resource-predator-prey systems (Rand and Wilson, 1995; Wilson and Keeling, 2000). Keeling *et al.* (1997) applied fluctuation analysis to three biological models: genetic selection, plant competition and a complex marine system. Data obtained from such models is fully spatially resolved and over long time series – an unlikely situation for any real system.

Although the models used in CLS studies are generally spatially explicit and are capable of nonlinear dynamics, they are not necessarily representative of dynamics in real systems. Smith (2000) points out that few models are well tested against reality. The major benefits of CLS techniques will come from their application to natural systems, in addition to models.

Directions

There is clearly a need to trial fluctuation analyses and determinism tests on data from real systems. However, while sufficient data may be available from measurements of neural activity, or of disease spread, it is unlikely that appropriate data can be obtained from natural ecosystems. Systems with high turnover rates could be an exception, although spatial data are generally difficult to collect from such systems. Mesocosms, or enclosed experimental ecosystems, can often be monitored more thoroughly than real systems (Petersen and Hastings, 2001). Such artificial systems might be a suitable compromise between model systems and natural systems for further investigation of CLSs.

A direct approach is to modify CLS estimation techniques so that their data requirements are more realistic. For their population genetics model, Wilson and Keeling (2000) used repeated spatial rather than temporal sampling. Windows were moved around the lattice until the full pattern had been sampled, and variance was calculated over the whole pattern at one point in time rather than for one fixed window over a time series. Wilson and Keeling (2000) do not indicate the method they used for repeated spatial sampling, or for calculating variances. Since they did not use attractor reconstruction for modeling average behaviours, their method is not appropriate for systems with oscillatory dynamics.

Johnson (2002) suggests that the techniques of Keeling *et al.* (1997) and of Pascual and Levin (1999) could be modified to use data from spatial rather than temporal sampling. Attractor reconstruction from a single "snap-shot" in time is theoretically possible if distant parts of a system are out of phase and therefore lie on separate parts of the attractor. Reconstruction would then be piece-wise. Such an approach would overcome the problem of attractors shifting in space through time. However, practical difficulties might arise with the process of embedding without a time series. Further investigation is needed to explore these possibilities.

ARE CLS MEASURES ROBUST?

Even if sufficient data could be obtained from natural systems to estimate CLSs, the usefulness of these measures would be reduced if they do not have some level of consistency when calculated for different components of a system, or for similar systems.

Robustness between components of a system

CLS estimation techniques examine the variance in a single component of a system. This is generally the density of one species, but it could also be the level of a resource or some other variable. Such an approach is suitable for a single species system (such as the model used by Tyre *et al.*, 1997), or if the aim is to determine the patch size of one species. However, for multi-species systems (studied by De Roos *et al.*, 1991; Rand and Wilson, 1995; Keeling *et al.*, 1997; Pascual and Levin, 1999; Wilson and Keeling, 2000) the choice of a component for calculating the CLS is relatively arbitrary.

In no cases have CLS estimates using different components of a system been compared. It seems fairly likely that different components of a model system would give different CLSs. This is even more probable in real systems, where species respond to different environmental factors. CLS estimates might relate to characteristics of the species used for analysis, particularly life history and relative abundance. Depending on the motivation for estimating the CLS, it may be more appropriate to use densities of a keystone species or a threatened species. It would be interesting to determine whether differences between CLS estimates from separate species are more or less pronounced with spatial rather than temporal replication.

Johnson (2002) emphasizes that the CLS for a *system*, rather than for a single species in the system, is often desirable. Johnson (2002) suggests the use of system level measures, such as multivariate statistics, to determine CLSs. This is another avenue for future investigation.

Robustness between related systems

CLSs are related to properties of the dynamics of a system. Accordingly, CLS estimates should be reasonably robust between related systems with similar dynamics. CLS measures should also

be robust to variation in the configuration of a system. Spatial models show that communities may have a wide range of possible configurations (Dunstan and Johnson; Johnson and Dunstan, submitted MS), and CLS estimates should be similar across these configurations. These issues have not been tested.

Environmental factors have not generally been considered in discussions of CLSs. One instance where they might be important is if two similar systems are subject to different environmental influences. Pascual and Ellner (2000) have described the challenge of incorporating specific environmental forcings into model systems. If successful, this might enable the effect of forcings on CLSs to be tested in model situations.

Schneider (1994) describes a real system example where physical factors complicate the estimation of characteristic patch sizes for phytoplankton. Patch size of phytoplankton is thought to be a response to the balance between opposing effects of cell division (which increases patchiness) and eddy diffusion (which disperses patches). However, density-dependent growth rates may depend on eddy diffusivity, so that growth balances eddy diffusivity at a shifting rather than a fixed scale. Levin (1992) argues that if interaction of biological with physical processes is the norm, then a shifting rather than characteristic scale can be expected in ecosystems.

Shifting scales, multiple scales or CLSs?

Various authors have asked whether there is a characteristic spatial scale on which to measure ecosystems, or if shifting or multiple characteristic scales should be expected (Addicott *et al.*, 1987; Levin, 1992; Schneider, 1994). Levin (1992) argues that rather than trying to determine the correct scale at which ecological phenomena should be studied, it is more important to understand how the system description changes across scales. Finding ways to relate dynamics across spatial scales is seen as a critical "next step" in ecology (Addicott et al., 1987; Pascala and Deutschman, 1995; Levin et al., 1997; Pascala and Levin, 1997; Law and Dieckmann, 2000; Levin, 2000). However, the detection of CLSs is a more important *practical* issue than understanding scaling relationships in ecosystems.

The CLS may not be the "correct" scale at which to view a system, but it is certainly a sensible intermediate window size for observation, between small windows where stochastic fluctuations dominate and large windows where interesting dynamics are averaged out. The question of whether CLSs are meaningful or not – for example whether they relate to other scaling characteristics of the system, or can be used to detect shifts in dynamics – has received little attention in the literature and is an obvious next step for future research.

CONCLUSIONS

The CLS is a useful intermediate scale at which to observe the dynamics of ecosystems. It is an inherent scale that gives the maximum amount of information about the system and its dynamics, relative to the quantity of data and work necessary to describe the system. The estimation of CLSs for natural systems has a wide range of applications: determining appropriate sampling scales for detecting trends in ecosystems; determining sizes for marine and terrestrial reserves; deciding scales for management units in ecosystems; and increased understanding of epidemiology and ecotoxicology.

Vegetation analysis methods developed between the early 1950s and late 1970s can be used to estimate patch sizes and investigate spatial patterns in ecosystems. In the last decade, investigators have looked at the dynamics of ecosystems through time to define CLSs. Fluctuation analysis (Keeling *et al.*, 1997) and determinism tests (Pascual and Levin, 1999) for estimating CLSs are attractive because they are appropriate to the complicated dynamics of some natural systems. However, when applied to identical data, these techniques suggest different CLSs. It is likely that fluctuation analysis and determinism tests give complementary information. Notably, neither technique has been applied to real systems.

The main problem with applying modern CLS measures to natural systems is that large quantities of data are required. While 'perfect' data can be obtained over long time periods from computer models, this is seldom true for real systems. A major challenge is to develop methods for estimating CLSs that require less data, for example by sampling repeatedly in space rather than

over time. The question of whether CLSs are robust to the species used, or to the system measured, remains largely unanswered.

Hill (1973) emphasized the importance of bridging the gap between mathematics and biology. It is important that CLS methodology is applied rather than just theoretical. Study of CLSs in natural systems should help in understanding the dynamics of ecosystems at different spatial scales. The issues of scale, space and dynamics in ecosystems are fascinating but are related in very complex ways that ecologists are only just beginning to appreciate. Tyre *et al.* (1997) claim that the search for CLSs is futile. This is certainly not the case; CLSs have been measured in model systems and there is great potential for modifying techniques for estimating CLSs so that they can be applied to real systems.

LITERATURE CITED

Abarbanel, H. D. I. 1996. Analysis of Observed Chaotic Data. Springer-Verlag, *New York.*

Addicott, J. F., Aho, J. M., Antolin, M. F., Padilla, D. K., Richardson, J. S. and Soluk, D. A. 1987. Ecological neighbourhoods: scaling environmental patterns. *Oikos* **49**, 340-346.

Carlile, D. W., Skalski, J. R., Batker, J. E., Thomas, J. M. and Cullinan, V. I. 1989. Determination of ecological scale. *Landscape Ecology* **2(4)**, 203-213.

Casdagli, M. 1989. Nonlinear prediction of chaotic time series. *Physica D* **35**, 335-356.

Cliff, A. D., Haggett, P., Ord, J. K., Bassett, K. A. and Davies, R. B. 1975. *Elements of Spatial Structure: A Quantitative Approach.* Cambridge University Press, Cambridge.

Crowley, P. H. 1977. Spatially distributed stochasticity and the constancy of ecosystems. *Bulletin of Mathematical Biology* **39**, 157-166.

Davis, J. C. 1986. *Statistics and Data Analysis in Geology.* John Wiley and Sons, New York.

Dent, C. L. and Grimm, N. B. 1999. Spatial heterogeneity of stream water nutrient concentrations over successional time. *Annals of Botany, New Series* **16**, 293-320.

De Roos, A. M., McCauley, E. and Wilson, W. G. 1991. Mobility versus density-limited predator-prey dynamics on different spatial scales. *Proceedings of the Royal Society of London B* **246**, 117-122.

Dunstan, P. and Johnson, C. R. 2002. Submitted MS.

Durrett, R. and Levin, S. 1994a. The importance of being discrete (and spatial). *Theoretical Population Biology* **46**, 363-394.

Durrett, R. and Levin, S. 1994b. Stochastic spatial models: a user's guide to ecological applications. *Philosophical Transactions of the Royal Society of London B* **343**, 329-350.

Durrett, R. and Levin, S. 1998. Spatial aspects of interspecific competition. *Theoretical Population Biology* **53**, 30-43.

Durrett, R. and Levin, S. 2000. Lessons on pattern formation from the planet WATOR. *Journal of Theoretical Ecology* **205**, 201-214.

Errington, J. C. 1973. The effects of regular and random distributions on the analysis of pattern. *Journal of Ecology* **61**, 99-105.

Ellner, S. and Turchin, P. 1995. Chaos in a noisy world: new methods and evidence from time-series analysis. *The American Naturalist* **145(3)**, 343-375.

Greig-Smith, P. 1952. The use of random and contiguous quadrats in the study of the structure of plant communities. *Annals of Botany, New Series* **16**, 293-320.

Greig-Smith, P. 1964. *Quantitative Plant Ecology*. University of California Press, Berkeley.

Goodall, D. W. 1974. A new method for analysis of spatial pattern by random pairing of quadrats. *Vegetatio* **29**, 135-146.

Hill, M. O. 1973. The intensity of spatial pattern in plant communities. *Journal of Ecology* **61**, 225-235.

Johnson, A. R. 2002. Landscape ecotoxicology and assessment of risk at multiple scales. *Human and Ecological Risk Assessment* **8(1)**, 127-146.

Johnson, C. R. 1997. Self-organizing in spatial competition systems. In *Frontiers in Ecology* (ed. N. Klomp and I. Lunt), pp. 245-263. Elsevier, Oxford.

Johnson, C. R. 2002. ARC application.

Johnson, C. R. and Dunstan, P. 2002. Submitted MS.

Jumars, P. A., Thistle, D. and Jones, M. L. 1977. Detecting two-dimensional spatial structure in biological data. *Oecologia* **28**, 109-123.

Kaplan, D. and Glass, L. 1995. *Understanding Nonlinear Dynamics*. Springer-Verlag, New York.

Keeling, M. J., Mezic, I., Hendry, R. J., McGlade, J. and Rand, D. A. 1997. Characteristic length scales of spatial models in ecology via fluctuation analysis. *Philosophical Transactions of the Royal Society of London B* **352**, 1589-1601.

Kershaw, K. A. 1957. The use of cover and frequency in the detection of pattern in plant communities. *Ecology* **38**, 291-299.

Law, R. and Dieckmann, U. 2000. A dynamical system for neighbourhoods in plant communities. *Ecology* **81(8)**, 2137-2148.

Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* **73**, 1943-1967.

Levin, S. A. 2000. Multiple scales and the maintenance of biodiversity. *Ecosystems* **3**, 498-506.

Levin, S. A. and Buttel, L. 1987. *Measures of Patchiness in Ecological Systems*. Publication ERC-130, Ecosystem Research Center, Cornell University, Ithaca.

Levin, S. A., Grenfell, B. Hastings, A. and Perelson, A. S. 1997. Mathematical and computational challenges in population biology and ecosystems science. *Science* **275**, 334-343.

Ludwig, J. A. 1979. A test of different quadrat variance methods for the analysis of spatial pattern. In *Spatial and Temporal Analysis in Ecology* (ed. R. M. Cormack and J. K. Ord), pp. 289-304. International Co-operative Publishing House, Fairland.

Ma, S. 1976. *Modern Theory of Critical Phenomena*. Addison-Wesley, New York.

Moloney, K. A., Levin, S. A., Chiariello, N. R. and Buttel, L. 1992. Pattern and scale in a serpentine grassland. *Theoretical Population Biology* **41**, 257-276.

Nichols, J. M. and Nichols, J. D. 2001. Attractor reconstruction for non-linear systems: a methodological note. *Mathematical Biosciences* **171**, 21-32.

O'Neill, R. V., Gardner, R. H., Milne, B. T., Turner, M. G. and Jackson, B. 1991. Heterogeneity and spatial hierarchies. In *Ecological Heterogeneity* (ed. J. Kolasa and S. T. A. Pickett). Springer-Verlag, New York.

Palmer, M. W. 1988. Fractal geometry: a tool for describing spatial patterns of plant communities. *Vegetatio* **75**, 91-102.

Pascala, S. W. and Deutschman, D. H. 1995. Details that matter: the spatial distribution of individual trees maintains forest ecosystem function. *Oikos* **74**, 357-365.

Pascala, S. W. and Levin, S. A. 1997. Biologically generated spatial pattern and the coexistence of competing species. In *Spatial Ecology: the Role of Space in Population Dynamics and Interspecific Interactions* (ed. D. Tilman and P. Karieva), pp. 201-232. Princeton University Press, Princeton.

Pascual, M. and Levin, S. A. 1999. From individuals to population densities: searching for the intermediate scale of nontrivial determinism. *Ecology* **80(7)**, 2225-2236.

Pascual, M. and Ellner, S. P. 2000. Linking ecological patterns to environmental forcing via nonlinear time series models. *Ecology* **81(10)**, 2767-2780.

Pascual, M. Mazzega, P. and Levin, S. A. 2001. Oscillatory dynamics and spatial scale: the role of noise and unresolved pattern. *Ecology* **82(8)**, 2357-2369.

Pei, X. and Moss, F. 1996. Characterization of low-dimensional dynamics in the crayfish caudal photoreceptor. *Nature* **379**, 618-621.

Peterson, J. E. and Hastings, A. 2001. Dimensional approaches to scaling experimental ecosystems: designing mousetraps to catch elephants. *The American Naturalist* **157(3)**, 324-333.

Platt, T. and Denman, K. L. 1975. Spectral analysis in ecology. *Annual Review of Ecology and Systematics* **5**, 189-210.

Powell, T. M. 1989. Physical and biological scales of variability in lakes, estuaries, and the coastal ocean. In *Perspectives in Ecological Theory* (ed. J. Roughgarden and R.M. May), pp. 157-176. Princeton University Press, Princeton.

Rand, D. A. 1994. Measuring and characterizing spatial patterns, dynamics and chaos in spatially extended systems and ecologies. *Proceedings of the Royal Society of London A* **348**, 497-514.

Rand, D. A. and Wilson, H. B. 1995. Using spatio-temporal chaos and intermediate-scale determinism to quantify spatially extended ecosystems. *Proceedings of the Royal Society of London B* **259**, 111-117.

Ripley, B. D. 1978. Spectral analysis and the analysis of pattern in plant communities. *Journal of Ecology* **66**, 965-981.

Rossi, R. E., Mulla, D. J., Journel, A. G. and Franz, E. H. 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. *Ecological Monographs* **62(2)**, 277-314.

Schneider, D. C. 1994. *Quantitative Ecology: Spatial and Temporal Scaling*. Academic Press, San Diego.

Smith, H. F. 1938. An empirical law describing heterogeneity in the yields of agricultural crops. *Journal of Agricultural Science* **28**, 1-23.

Smith, J. 2000. Nice work – but is it science? *Nature* **408**, 293.

Sokal, R. R. and Oden, N. L. 1978a. Spatial autocorrelation in biology 1. Methodology. *Biological Journal of the Linnean Society* **10**, 199-228.

Sokal, R. R. and Oden, N. L. 1978b. Spatial autocorrelation in biology 2. Some biological implications and four applications of evolutionary and ecological interest. *Biological Journal of the Linnean Society* **10**, 229-249.

Takens, F. 1981. Detecting strange attractors in turbulence. In *Dynamical Systems and Turbulence, Warwick, 1980. Lecture Notes in Mathematics* ***898*** (ed. D. Rand and L. S. Young), pp. 366-381. Springer-Verlag, New York.

Turner, S. J., O'Neill, R. V., Conley, M. R., and Humphries, H. C. 1991. Pattern and scale: statistics for landscape ecology. In *Quantitative Methods in Landscape Ecology* (ed. S. J. Turner and R. H. Gardner), pp. 17-49. Springer-Verlag, New York.

Tyre, A. J., Possingham, H. P. and Bull, C. M. 1997. Characteristic scales in ecology: fact, fiction or futility. In *Frontiers in Ecology* (ed. N. Klomp and I. Lunt), pp. 233-243. Elsevier, Oxford.

Usher, M. B. 1969. The relation between mean square and block size in the analysis of similar patterns. *Journal of Ecology* **57**, 505-514.

Usher, M. B. 1975. Analysis of pattern in real and artificial plant populations. *Journal of Ecology* **63**, 569-586.

Wiegert, R. G. 1962. The selection of an optimum quadrat size for sampling the standing crop of grasses and forbs. *Ecology* **43**, 125-129.

Wilson, H. B. and Keeling, M. J. 2000. Spatial scales and low-dimensional deterministic dynamics. In *The Geometry of Ecological Interactions: Simplifying Spatial Complexity* (ed. U. Dieckmann, R. Law and J. A. J. Metz), pp. 209-226. Cambridge University Press, Cambridge.

Zöller, G., Engbert, R., Hainzl, S. and Kurths, J. 1998. Testing for unstable periodic orbits to characterize spatiotemporal dynamics. *Chaos, Solitons and Fractals* **9(8)**, 1429-1438.